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THE 1980 SINO-AMERICAN BOTANICAL EXPEDITION TO WESTERN HUBEI PROVINCE, PEOPLE'S REPUBLIC OF CHINA

B. BARTHOLOMEW, D. E. BOUFFORD, A. L. CHANG, Z. CHENG,
T. R. DUDLEY, S. A. HE, Y. X. JIN, Q. Y. LI,
J. L. LUTEYN, S. A. SPONGBERG, S. C. SUN,
Y. C. TANG, J. X. WAN, AND T. S. YING

THE BOTANICAL SOCIETY OF AMERICA'S Committee for Scientific Liaison with the People's Republic of China, chaired by Peter H. Raven, director of the Missouri Botanical Garden, and a corresponding committee of botanists in the People's Republic of China, chaired by Tang Pei-sun, director of the Institute of Botany, Academia Sinica, Beijing, successfully sponsored and arranged exchange visits of American botanists to the People's Republic of China in 1978, and Chinese botanists to the United States in 1979. These delegations were limited to visiting botanical institutions, and the exchange resulted in a basic understanding by the participants of the current status of botanical research in both countries (see Thorhaug, 1978; Bartholomew, Howard, & Elias, 1979; Howard, Bartholomew, & Elias, 1979). At the conclusion of the visit by the Chinese delegation to the United States in early June of 1979, a meeting was convened at the University of California, Berkeley, to discuss the kinds of cooperative programs that might be developed in the future. The general consensus of the participants at that meeting was that steps should be taken to promote cooperative ventures beyond the delegation level, and that joint participation in botanical research was highly desirable.

As a direct result of the Berkeley meetings, five American botanists were invited by the Academia Sinica to participate in a botanical expedition in China with Chinese colleagues. In return, five Chinese botanists were invited to the United States for a one-year period to study at botanical institutions and to take part in fieldwork. The purpose of this report is to summarize the activities and results of the 1980 Sino-American expedition, the first joint

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botanical expedition involving botanists from the United States and the People's Republic of China since the founding of the People's Republic in 1949.

The 1980 Sino-American Botanical Expedition to western Hubei[1] Province was conducted under the auspices of the Academia Sinica and the Botanical Society of America and consisted of a three-month (15 August–15 November 1980) visit to the People's Republic by the American participants. Professor S. C. Sun, director of the Wuhan Institute of Botany and chairman of the Department of Biology, Wuhan University, was the expedition leader. Most of the field investigations were conducted in the Shennongjia Forest District in western Hubei Province, with additional fieldwork in the metasequoia region of Lichuan Xian in southwestern Hubei. The herbarium collections made in both areas are enumerated in the list presented below, but a report of the brief visit to the metasequoia region is presented in a separate paper (Bartholomew, Boufford, & Spongberg, 1983) that follows this report.

Once the fieldwork had been concluded, the American participants visited several botanical institutions and botanical gardens throughout China before returning to the United States. During that period, time was available for individual study in the herbaria and libraries and for observation and discussion of the research being conducted in those institutions.

The following sections summarize the ecological, physical, and climatic conditions of the Shennongjia Forest District, previous botanical exploration in the area, and observations on current lumbering practices in the region. A list of determinations of the collections concludes this report. During the six weeks spent in the field, 2085 collections were made, of which 1715 numbers represent vascular plants. A separate report concerning the collections of nonvascular plants is planned.

NATURAL CONDITIONS IN THE SHENNONGJIA FOREST DISTRICT

GEOGRAPHIC POSITION. The Shennongjia Forest District (MAP 1), with an area of about 3250 km^2 (slightly larger than the state of Rhode Island, and almost exactly the same size as Yosemite National Park, in the United States), is situated at 31°15′–31°57′ north latitude and 109°56′–110°58′ east longitude. It lies in the northwestern part of Hubei Province and is bounded on the west by Sichuan Province. The district was created in 1970 from what were parts of Badong Xian (county), Xingshan Xian, and Fang Xian and was set off as a separate administrative division at the level of xian.

GEOLOGY AND GEOMORPHOLOGY. The Shennongjia Mountains are an extension of the southeastern Dabashan Mountain system, a subrange of the Wushan Mountains (Ying *et al.*, 1979). The region was gradually uplifted in the middle Devonian and was formed into a mountain body through the Yanshan, and then the Himalayan, mountain movements, with rising continuing after these movements. As a result of strong, constant erosion that kept pace with the

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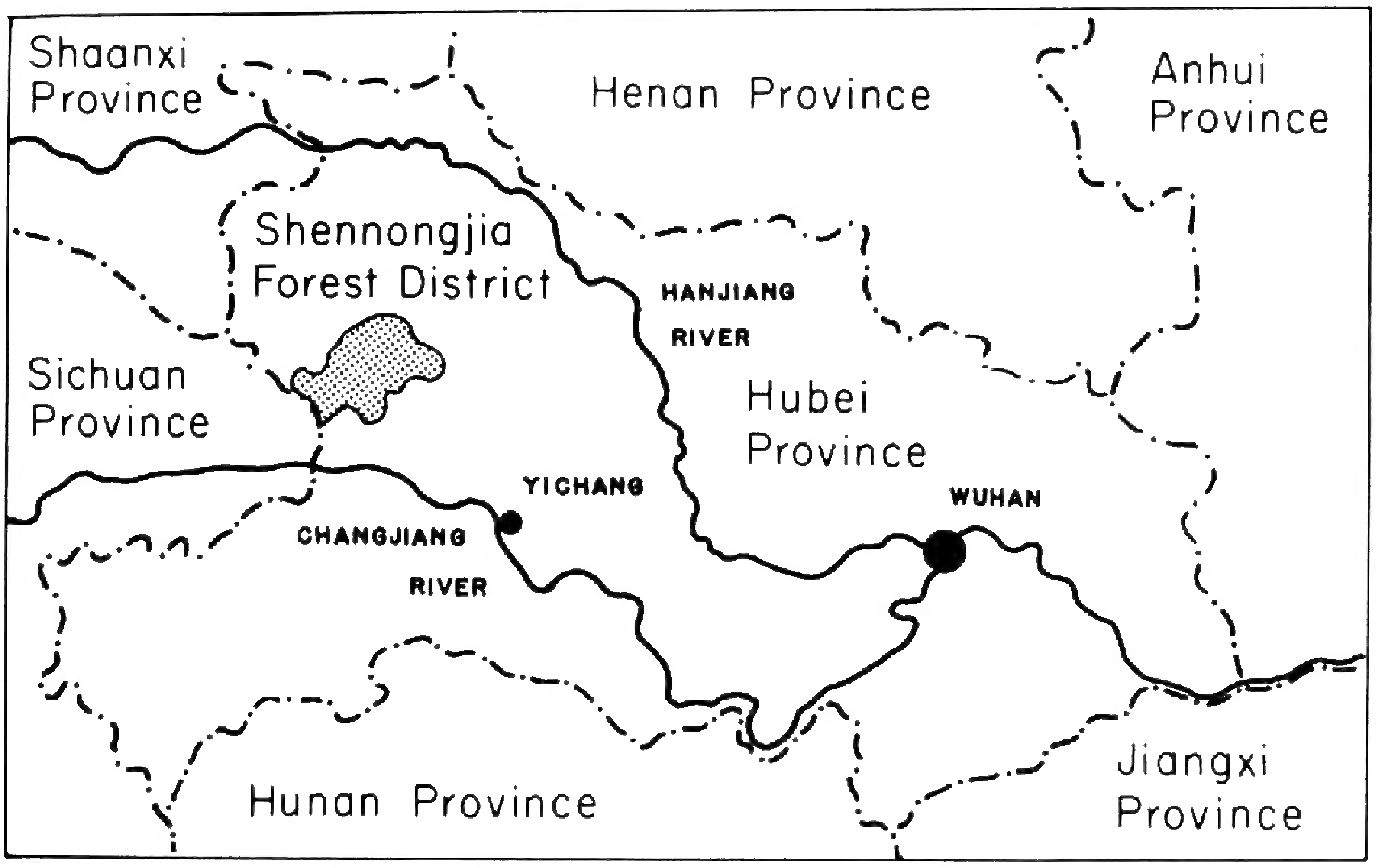
[1] The Pinyin system of romanization is used throughout except for names of older collectors, authors, and places for which changes in spelling might cause confusion. In these instances the Wade-Giles spelling is given in parentheses.



MAP 1. Outline of Hubei Province indicating location of Shennongjia Forest District (stippled).

uplift, the range appears young geologically, as evidenced by high mountains, deep valleys, and steep slopes (FIGURE 1). In some areas a karst topography has developed. The rock formation consists primarily of sedimentary rock (mainly Sinian siliceous limestone, Cambrian and Ordovician limestone and shale, Silurian calcareous shale, and Tertiary sandstone) interspersed with some metamorphic rock. Quaternary sediments are undeveloped.

The mountains in the Shennongjia Forest District are oriented in a nearly west-southwest to east-northeast direction and have an average elevation of around 1800 meters. The main mountain peaks are located slightly south of the central part of the district and include Laojun-shan (2936 m), Xiaoshennongjia (3005 m), Dashennongjia (3052 m), and Wuming Peak (3105 m), the highest in Shennongjia. However, the areas along the river valleys, such as along the Yangriwan and Yinyu-he rivers, are at an elevation of only several hundred meters. The altitudinal differences between these areas and the main peaks are usually more than 2000 meters. Many deeply incised, V-shaped valleys occur in Shennongjia, forming a radiate drainage pattern (see MAP 2), with the water flowing into the Changjiang (Yangtze) and Hanjiang (Han) rivers (the Songlo-he and Nicha-he rivers in the north and the Yinyu-he and Loyang-he rivers in the west flow into the Hanjiang; the Jiuchong-he and Dangyang-he in the southeast and the Yandu-he in the southwest flow into the Changjiang).

CLIMATE. Shennongjia is situated in a transitional area between the higher mountains of southwestern China and the low, hilly regions of the southeastern part of the country, and its climate is characteristic of an east-west transitional zone. It also lies in the path of monsoons moving north. Moreover, due to the topographical features of high, steep mountains and deeply incised valleys, the microclimates in the areas that we explored vary greatly, providing habitats

FIGURES 1, 2. Shennongjia Forest District: 1, view southwest from Xiaoshennongjia, ca. 3000 m alt., showing succession of mountain ridges, rough terrain, and steep topography of Forest District; 2, upper montane vegetation on Xiaoshennongjia, ca. 3000 m alt. (note thickets of *Sinarundinaria nitida* in right foreground; prominent conifer, *Abies fargesii*).

TABLE 1. **Meteorologic data for Songbaizhen and Dajiuhu, Shennongjia Forest District.**

STATION & ELEVATION	TEMPERATURE (°C)					NO. OF FROST-FREE DAYS PER YEAR	ANNUAL PRE-CIPITATION (in mm)
	Mean annual	Mean January	Mean July	Minimum	Maxi-mum		
Songbaizhen, 935 m	12.2	1.0	23.5	−17.7	36.4	227	973.7
Dajiuhu, 1700 m	7.4	−4.9	18.5	−21.2	34.5	144	1528.4

that range from warm temperate–subtropical at the lowest elevations to essentially boreal at the summits of the highest peaks. Weather stations were only recently established in this district, but there are not enough of them to provide detailed climatic data for much of the area. The data in TABLE 1 are based on meteorologic observations recorded at Songbaizhen (935 m alt.) and Dajiuhu (1700 m alt.) and made available by the Meteorologic Service of the Shennongjia Forest District.

Based on the available meteorologic data, the climate of Shennongjia appears to be warm temperate to temperate, with an abundance of moisture. There is far too little information from the areas along the river valleys at low elevations and from the highest peaks, but based on the distribution of the vegetation it is apparent that the lowest elevations support a few subtropical taxa while the highest elevations are occupied almost exclusively by boreal elements.

SOILS. There are three main types of soil, which are vertically distributed in Shennongjia (Ying *et al.,* 1979): a yellow-brown forest soil belt, a mountain brown forest soil belt, and a mountain gray-brown forest soil belt.

The yellow-brown forest soil belt is found at elevations below 1500 meters. The parent materials forming this soil are mostly purple and red arenaceous shale (pH 6–7). Organic materials are thoroughly decomposed due to the moisture/heat conditions and the wet and dry seasons.

The mountain brown forest soil belt occupies a position between 1500 and 2200 meters elevation. The parent materials are mainly limestone, micaceous sandstone, and quartz-containing sandstone (pH 4.5–6). This belt is densely covered with vegetation and has a rather good accumulation of humus.

The mountain gray-brown forest soil belt is located at elevations above 2200 meters. The parent materials are limestone and quartz-containing sandstone (pH 4.5–6.5). The organic layer is well developed.

FLORA AND VEGETATION. The floristic and vegetational characteristics of Shennongjia have been discussed to a greater or lesser extent by Peng (1957), Wu (1979, 1980), Ying *et al.* (1979), and Ban (1980). However, we would like to comment on aspects of the flora and vegetation in the areas that we visited.

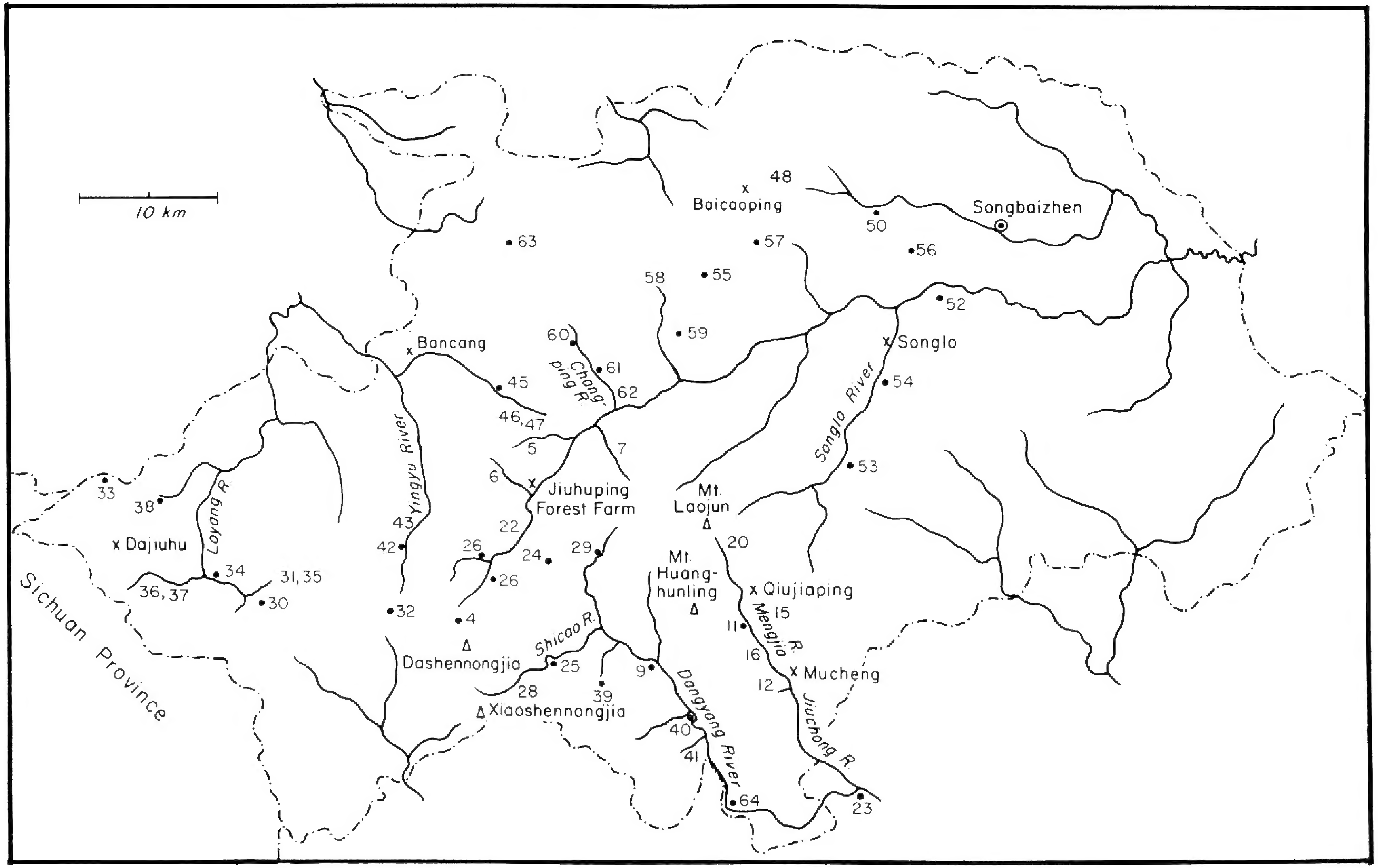
Natural vegetation predominates over much of the area but is being altered at an alarming rate. At lower elevations (generally below 1800 m) much of the natural vegetation has already been totally destroyed for timber or to provide crop land. Virgin forests are for all practical purposes nonexistent, although there are a few areas at middle elevations that support well-developed secondary forests containing a rich variety of tree species, and there are some relatively undisturbed coniferous forests at the highest elevations. Nevertheless, even these areas are being exploited at a rapid rate, and many steep slopes at middle and high elevations have been completely stripped of forest cover. This practice has led to serious erosional problems, which will definitely worsen as more areas are cut.

Coniferous forests are far less extensive than broad-leaved forests, due partly to the fact that coniferous forests that have been lumbered have mostly been replaced by broad-leaved ones. Except in certain areas at high elevations (e.g., on Mts. Laojunshan and Xiaoshennongjia; see FIGURE 2), pure, intact, coniferous forests are scarce.

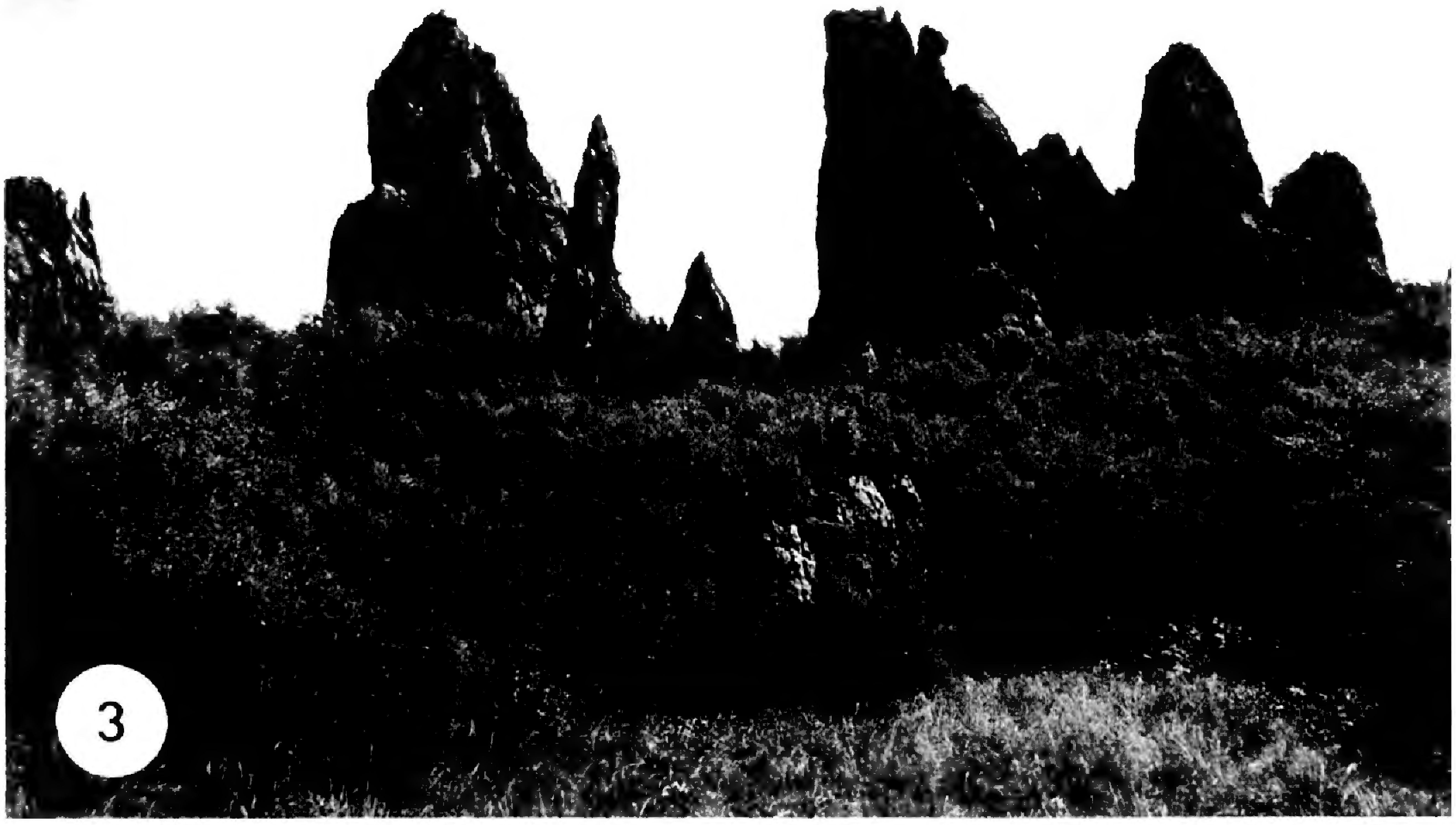
Vertical zonation of the forests in Shennongjia is not easily observable. The original vegetation does not cover large areas, and it is difficult to distinguish the upper and lower boundaries of the various vegetation types. Some idea of the altitudinal zonation can be achieved by piecing together data from various parts of the district, but this may not reflect the true distribution of the original forest components (however, see Ying *et al.*, 1979).

The main vegetational patterns in Shennongjia can be classified into at least seven associations: evergreen broad-leaved forest, mixed evergreen and deciduous broad-leaved forest, dwarf bamboo thickets of *Sinarundinaria nitida* (FIGURE 3), deciduous broad-leaved forest (FIGURE 4), pine forest (either *Pinus armandii* or *P. massoniana*), boreal hardwood forest (consisting of *Betula* spp., *Sorbus* spp., *Acer* spp., and scattered gymnosperms, especially *Abies*), and fir forests (comprised almost exclusively of *Abies fargesii*). In addition, there are the different plant communities present in the subalpine-alpine meadows, the fens, and the marshes, as well as on the numerous vertical cliffs (FIGURE 5) located throughout the district.

The complex topography, the wide differences in climate, the geographic position, and the floristic history of the Shennongjia region have resulted in the development of a rich and varied flora (which includes a number of relict families, genera, and species) in the area. Based on Anonymous (1980) and additions to the flora collected during the 1980 Sino-American Botanical Expedition, the vascular flora comprises 2090 species in 786 genera and 166 families. Of these, 64 families and 307 genera are primarily represented in the tropics and subtropics, while 61 families and 304 genera belong to groups that are predominantly temperate in distribution. However, only 21 families and 98 genera are mostly restricted to the tropics, leaving subtropical and temperate groups as the major components of the flora. This breakdown by larger taxonomic groupings does not give a clear picture of the actual situation. Of the subtropical elements, most of the families and genera are represented by only one or a few species, while in the primarily temperate groups the genera and families are often represented by several to many species. Examples of these include *Dryopteris* (15 spp.), *Polystichum* (19 spp.), *Salix* (16 spp.), *Betula* (6



MAP 2. Shennongjia Forest District: collecting localities of the 1980 Sino-American Botanical Expedition. Numbers correspond to collection localities (see APPENDIXES 1, 2), dots show exact localities, numbers not associated with dots indicate collecting areas. Unnumbered collection localities are in vicinity of place names.



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FIGURES 3, 4. Shennongjia Forest District: 3, *Sinarundinaria nitida* forming dense, impenetrable thickets at ca. 2650 m alt. at Banbiyon (rock formation characteristic of many areas of region); 4, Loyang River gorge near Pingqian at 1300 m alt. (forest on slopes above river composed largely of *Tsuga chinensis, Tetracentron, Cercidiphyllum, Acer robustum, Davidia, Pterocarya paliurus, Fagus* spp., and *Malus* sp.).

spp.), *Carpinus* (9 spp.), Ranunculaceae (63 spp.), *Sorbus* (8 spp.), *Cotoneaster* (13 spp.), *Acer* (18 spp.), *Rhododendron* (14 spp.), and *Viburnum* (17 spp.).

The flora of Shennongjia is more similar to those of eastern and northeastern China and Japan than to that of southwestern or southern China. Many genera extend from eastern Sichuan–western Hubei into eastern China and to Japan (Ying *et al.*, 1979). Examples of plants with this distribution pattern are *Pleurosoriopsis* (Pleurosoriopsidaceae); *Akebia* (Lardizabalaceae); *Deinanthe, Rodgersia,* and *Schizophragma* (Saxifragaceae); *Paulownia* (Scrophulariaceae); *Weigela* (Caprifoliaceae); *Peracarpa* (Campanulaceae; extending to the Himalayas); *Euptelea* (Eupteleaceae); *Cercidiphyllum* (Cercidiphyllaceae); *Hosta, Reineckea, Tricyrtis,* and *Cardiocrinum* (Liliaceae); *Epimedium* (Berberidaceae); and *Aucuba* and *Helwingia* (Cornaceae; both extending to the Himalayas). In addition, many species in more widely ranging genera occur only in the region extending from central China to Japan.

A smaller number of genera are related to groups more characteristic of the Himalayan region or of regions more to the south or west. These include *Holboellia* and *Decaisnea* (Lardizabalaceae), *Brandisia* (Scrophulariaceae), *Streptolirion* (Commelinaceae; also extending to Korea), *Tupistra* (Liliaceae), and *Gastrochilus* (Orchidaceae).

Another group of plants in the Shennongjia Forest District includes those belonging to genera showing disjunct distribution between eastern Asia and eastern North America. Examples are *Matteuccia* (Onocleaceae), *Maclura* (Moraceae), *Caulophyllum* and *Diphylleia* (Berberidaceae), *Buckleya* (Santalaceae), *Antenoron* (Polygonaceae), *Liriodendron* (Magnoliaceae), *Illicium* (Illiciaceae), *Schisandra* (Schisandraceae), *Sassafras* (Lauraceae), *Stylophorum* (Papaveraceae), *Decumaria* and *Penthorum* (Saxifragaceae), *Pachysandra* (Buxaceae), *Acer* sect. NEGUNDO (Aceraceae), *Cryptotaenia* (Umbelliferae), *Lyonia* and *Vaccinium* sect. HUGERIA (Ericaceae), *Trachelospermum* (Apocynaceae), *Catalpa* (Bignoniaceae), *Phryma* (Phrymaceae), *Triosteum* (Caprifoliaceae), and *Aletris* (Liliaceae).

There are also a number of genera endemic to central, or central and southwestern, China (Li, 1953) that are represented in the flora of Shennongjia. Some of these are *Pteroceltis* (Ulmaceae), *Saruma* (Aristolochiaceae), *Tetracentron* (Tetracentraceae), *Asteropyrum* (Ranunculaceae), *Sargentodoxa* (Sargentodoxaceae), *Sinofranchetia* (Lardizabalaceae), *Eucommia* (Eucommiaceae), *Sinowilsonia, Sycopsis,* and *Fortunearia* (Hamamelidaceae), *Dipteronia* (Aceraceae), *Clematoclethra* (Actinidiaceae), *Davidia* (Nyssaceae, or Davidiaceae), *Dipelta* and *Kolkwitzia* (Caprifoliaceae), *Emmenopterys* (Rubiaceae), and *Ischnogyne* (Orchidaceae).

Continental glaciers did not encroach upon all of the Shennongjia region during the Quaternary (Li, 1940), and it is thought that this may have allowed a number of relict genera and families to survive there. However, it is also possible that many of these plants could have migrated southward during the Pleistocene, returning only after the climate warmed at the end of the last glaciation.

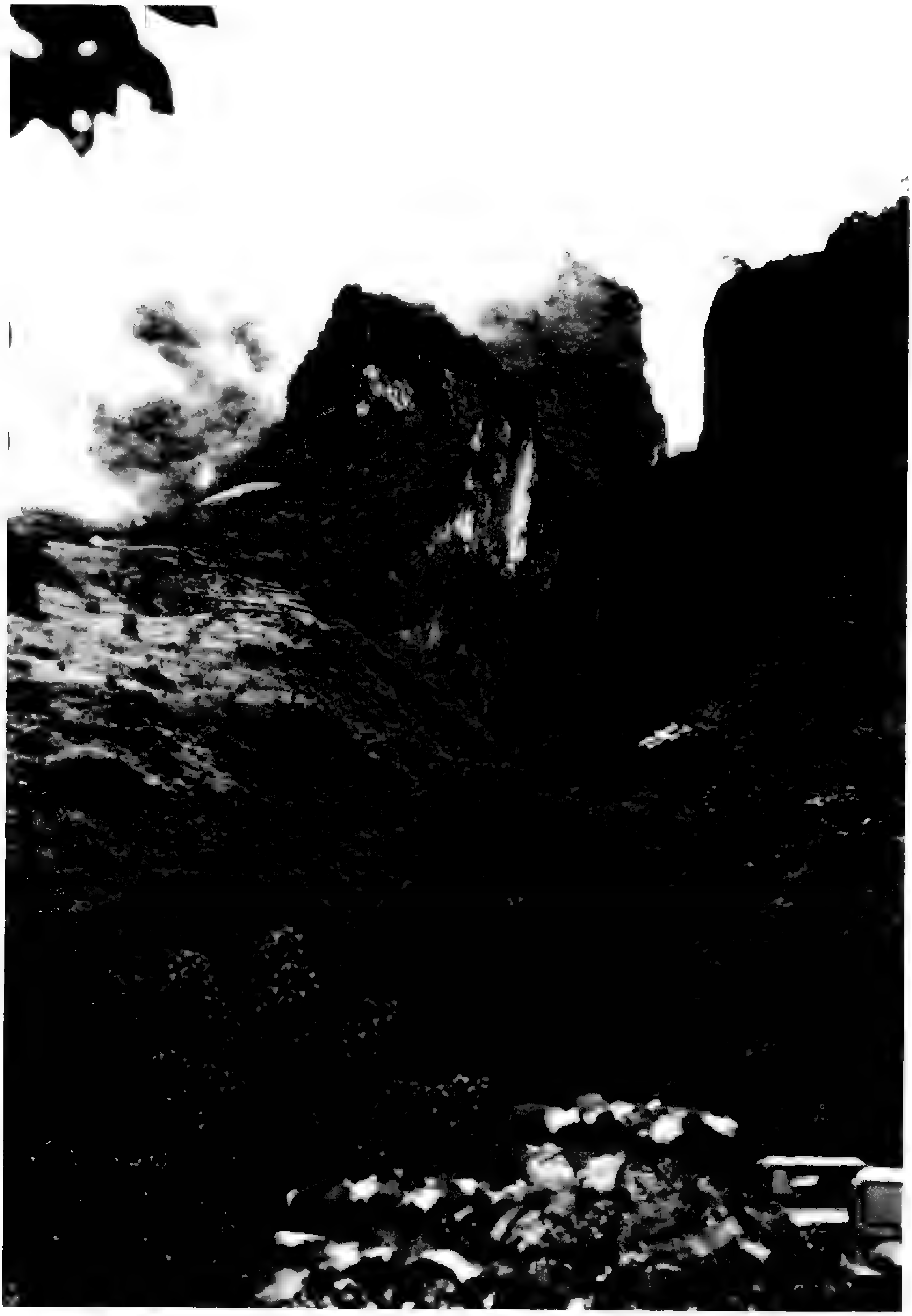

FIGURE 5. Shennongjia Forest District: steep, nearly vertical cliffs (ca. 400 m alt. at base) close to southern boundary of Forest District near confluence of Jiuchong and Dangyang rivers. Slopes support rich broadleaved-evergreen mixed deciduous forest association (but note corn field on slope at middle left).

MAN'S INFLUENCE ON THE REGION

Since the Shennongjia Forest District contains some of the roughest terrain in Hubei Province, the vegetation has until recently remained unexploited. However, the demand for lumber and other forest products in the People's Republic has increased to the extent that even remote areas of the District are currently being made accessible. Areas at lower elevations and forests on moderate slopes had been largely lumbered prior to the 1980 expedition (FIGURE 6). In 1980 roads were in place, or under construction, into high mountain regions and areas of extremely rough topography; large tracts of forested land, including areas on the steepest slopes, were being clear-cut. The timber is removed from these sites by sliding the logs down the steep slopes to collecting and loading areas, resulting in serious erosion. Cables suspended across valleys facilitate removal of logs from more inaccessible locations. From collection points the timber is transported by truck to larger collection depots, or "forest farms" (for example, our primary base camp was Jiuhuping Forest Farm; see MAP 2), where some of the logs are cut into boards for local use. Most of the logs, however, are taken to the Changjiang (Yangtze) River for transport as giant rafts downstream to eastern China, where the timber is processed for use.

Although our party was unable to visit all areas of the Shennongjia Forest District, and although none of us professes a thorough knowledge of forestry, we were nonetheless struck by the alarming rate at which both lumbering and preparation for future cutting were progressing. If cutting continues at the present rate, it might be roughly estimated that the forests of the district will be depleted of useful timber within a ten-year period. Of equal concern was the apparent waste evident in the lumbering process, the general disregard for the vegetation as a whole (through clear-cutting and the log slides), and the apparent lack of reforestation. In 1980 many of the areas that had been lumbered were under cultivation in food crops, and it was incredible to observe corn "fields" on slopes at angles greater than 45°. The yield in these fields is very low: in many areas the stalks produce no ears or only a single one. It is obviously very expensive to remove timber from the district. If this is to remain as a major timber-producing region, the expansion of the human population into the lumbered areas—especially those more readily accessible at low elevations, where the yields could potentially be greatest—should be strongly discouraged. The middle and higher elevations should remain unpopulated since the land there appears unsuitable for agriculture. Reforestation of lumbered areas, both to prevent extensive erosion and to provide a more continuous yield of forest products, should be the first priority in the district. Altered lumbering procedures would also allow for natural reforestation with native species. The members of the 1980 expedition hope that man's presence in the district will be limited, and that steps will be taken to preserve representative vegetational areas within the area before they are completely destroyed.

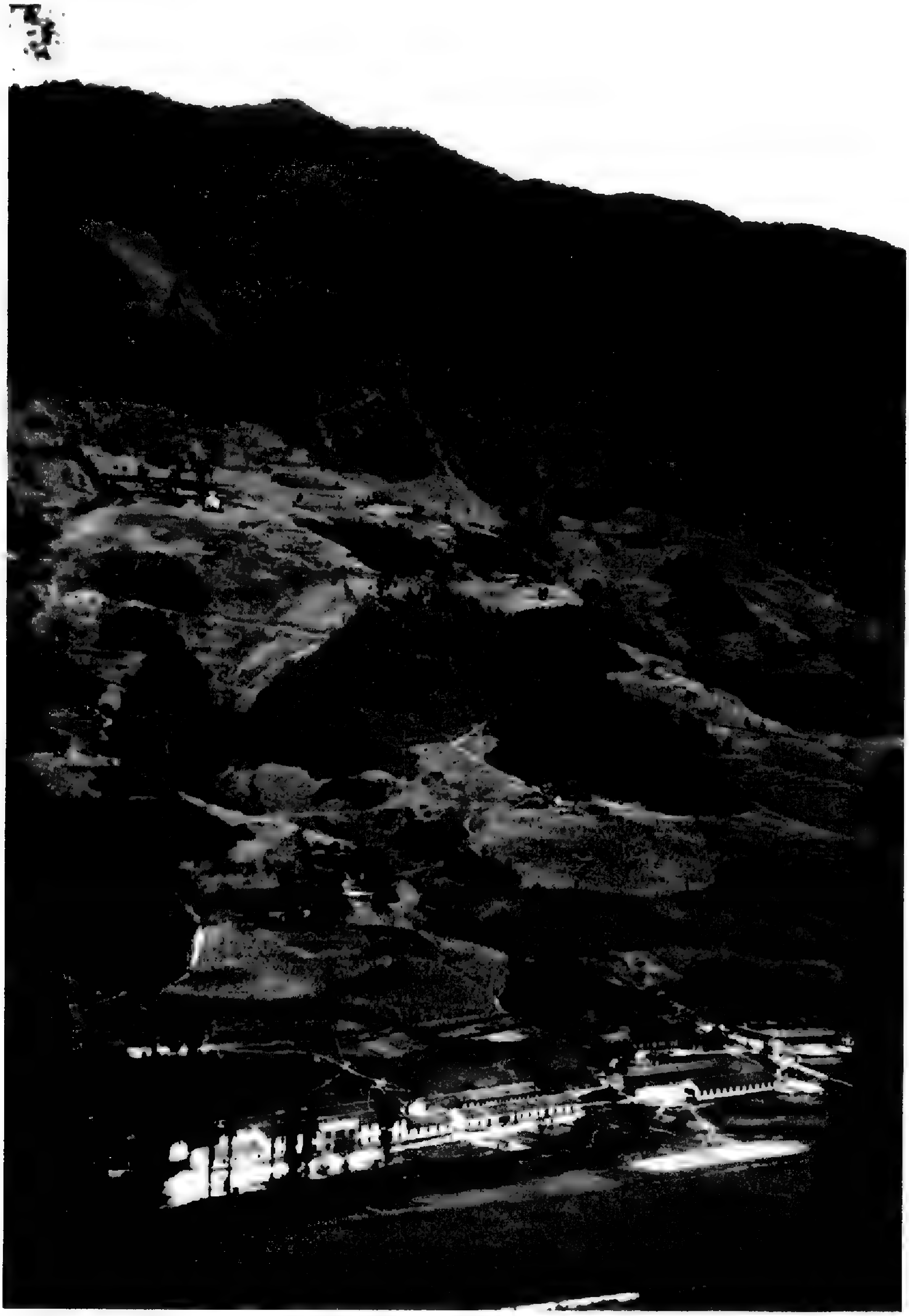

FIGURE 6. Shennongjia Forest District: Songlo Commune along the Songlo River at 1000 m alt. Lower- and middle-elevation slopes above commune buildings largely denuded of native vegetation and planted in corn; small groves of *Pinus massoniana* also planted for timber. Slender trees in front of commune, *Cunninghamia lanceolata*, with lateral branches pruned for firewood.

PREVIOUS BOTANICAL EXPLORATION IN THE SHENNONGJIA FOREST DISTRICT AND LICHUAN XIAN

So far as can be determined, the first botanical collections from within the region that now constitutes the Shennongjia Forest District were made by Augustine Henry, an Irish physician and botanist, during the period 1882–1889, when he was stationed as an officer of the Chinese Imperial Maritime Customs Service in Yichang (Ichang). Some of Henry's collections from the district were probably made by Chinese collectors in his employ, since his own collecting activities were initially concentrated within a ten- to fifteen-mile radius of Yichang (Bretschneider, 1898). However, in July of 1888, Henry made a trip to Baokang Xian (Paokang Hsien), Fang Xian, and Wushan Xian. In a letter to the director of the Royal Botanic Gardens, Kew, Henry recounted that on that journey he ". . . travelled due north from Ichang till I reached the range separating the basins of the Yangtze and Han Rivers, and then I made my way along the ranges westwards as far as Szechuan, striking then the Yangtze on the Hupeh-Szechuan boundary line I returned two or three days ago by boat down the rapids. . . . I reached at one point about 10,000 feet altitude, and found the mountains from 8,000 to 10,000 feet rich in plants not previously sent. . . . No foreigner, not even the Roman Catholic missionaries, had ever been in these parts before . . ." (Henry *in* Thiselton-Dyer, 1889, p. 226). From these excerpts of the letter as well as from some of the plants he mentioned, it is apparent that Henry had traveled across what is now part of the Shennongjia Forest District.

The second botanist to visit the region was E. H. Wilson, an English plant explorer, who began to collect in western Hubei and eastern Sichuan provinces early in 1900. Altogether, Wilson made four expeditions in China, the first two in the employ of the Veitch nursery firm of Chelsea, England, and the latter two under the auspices of the Arnold Arboretum (see Howard, 1980). The first two years of Wilson's initial expedition were spent exploring the mountains of western Hubei, and to judge from the map Wilson published of his itinerary (Wilson, 1905; see also Clausen & Hu, 1980), there is evidence that he also penetrated the Shennongjia region. Moreover, in his *A Naturalist in Western China* Wilson (1913) described in some detail a trip undertaken from Yichang to Daning (Taning) in Sichuan during the fourth expedition. Leaving Yichang on 4 June 1910 and traveling via Xingshan Xian, Wilson journeyed to Qingtianpao (Chin-tien-po), Xiaolongtan (Hsao-lung-tan), Dalongtan (Ta-lung-tan), and Dajiuhu (Ta-chu-hu), reaching Daning in 22 days. All four of these intermediate locations are today within the Shennongjia Forest District.

Although both Henry and Wilson undoubtedly prepared herbarium specimens of many of the plants they encountered while in the Shennongjia Forest District, the label data on their specimens are usually inadequate for pinpointing exact locations. As a result, it is usually impossible (particularly with Henry's specimens) to determine if a particular collection was made in the Shennongjia region.

The first Chinese botanists to collect in the Forest District were W. Y. Chun,

S. S. Chien, and R. C. Ching. These botanists left Yichang in July, 1922, and traveled via Wan-chao-shan (Wan-tsao-shan) in western Xingshan Xian to Xiaolongtan and Jiucaiyazi. Their two-month journey yielded more than 1000 numbers, but the most complete set was destroyed by fire in 1924 (R. C. Ching, pers. comm.). Some of the duplicate collections were distributed, however, and are in the herbaria of Nanjing University (N), the Institute of Botany, Beijing (PE), the Arnold Arboretum (A), and the United States National Herbarium (US). Likewise, a collection of nearly 3000 numbers made by Y. Chen in 1926 may include specimens from the Shennongjia Forest District, but since his field notes are missing it is impossible to determine exact localities for these specimens, which are deposited in the herbaria of Nanjing University (N) and Nanjing Technical College of Forest Products (NF).

In July and August of 1943, a forest survey was undertaken in the Shennongjia region and additional herbarium specimens were collected. It is of historical interest that C. Wang (T. Wang or Wang Zhan) participated in this survey and then undertook a side trip to Wan Xian (Wan Hsien) and Modaoqi (Mo-tao-chi), where he was the first botanist to collect specimens of *Metasequoia glyptostroboides.*

Subsequent to the early activities in the Shennongjia region in the 1920's and early 1940's, extensive botanical collections were made in the 1950's and particularly during the period 1976–1978 by the Shennongjia Plant Resources Expeditions. The participants of these expeditions analyzed the vegetation and plant resources of the region and collected more than 10,000 numbers (Anonymous, 1980). These collections, although distributed widely in herbaria throughout China, are deposited primarily in the herbaria of the Wuhan Institute of Botany (HIB) and the Institute of Botany, Beijing (PE).

The history of botanical exploration in Lichuan Xian, where *Metasequoia glyptostroboides* was discovered as an extant plant, has been summarized by Hu (1980) in her paper concerning the flora associated with *Metasequoia* and is outlined briefly by Bartholomew, Boufford, and Spongberg (1983). Among the more recent Chinese collectors to visit this area are C. Wang, C. Y. Hsüeh, C. T. Hwa, K. L. Chu, W. C. Cheng, and Y. W. Djou. Prior to the American scientists on the present expedition, the last ones to visit the region were R. W. Chaney and J. L. Gressitt, whose activities in the area were prompted by the discovery of *Metasequoia.*

As far as can be determined, the American participants in the 1980 Sino-American Botanical Expedition to western Hubei were the first Western botanists to collect in the Shennongjia Forest District since the days of E. H. Wilson, and in the metasequoia area of Lichuan Xian since Chaney and Gressitt. Although the activities of Chinese botanists have greatly increased our knowledge of the floras of both regions (Anonymous, 1976, 1979, 1980), it is significant that 15 taxa new to science (13 new species, 1 variety, and 1 forma) are proposed as a result of the 1980 expedition, and that numerous taxa from both Shennongjia and the metasequoia region are recorded from these areas for the first time. Although it can safely be said that the flora of western Hubei is relatively well known, our knowledge still remains incomplete.

ACKNOWLEDGMENTS

We would like to express our gratitude and thanks to the many people, too numerous to mention, who gave freely of their time and advice in the planning and execution of the expedition, as well as to those who helped to prepare this report. Primary responsibility for this paper is shared by D. E. Boufford and S. A. Spongberg, who either wrote or edited sections of the manuscript prepared by Chinese and American participants. In China S. C. Sun and Y. C. Tang rendered similar service. Our thanks are also expressed to C. Z. Ji, who skillfully prepared the illustrations of the new taxa of pteridophytes. The help of M. Byrnes in the preparation of the manuscript and of E. B. Schmidt in its editing is also gratefully acknowledged.

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AN ENUMERATION OF THE VASCULAR PLANTS COLLECTED ON THE 1980 SINO-AMERICAN BOTANICAL EXPEDITION TO WESTERN HUBEI

The following annotated list represents the determinations of the vascular plants collected both in the Shennongjia Forest District (numbers *1–1924*) and in the metasequoia region of Lichuan Xian (numbers *1925–2085*). Numbers between *1* and *2085* not represented in this list were assigned to nonvascular plants that will be detailed elsewhere. Names followed by an asterisk indicate taxa previously unreported for the Shennongjia Forest District, based on *Shennongjia Plants* (Anonymous, 1980).

Determinations of the collections were undertaken by both American and Chinese participants of the expedition, and lists of determinations were exchanged for comparison as the work progressed. Discrepancies were evaluated in herbaria in both the People's Republic of China and the United States until agreement was reached. In the few instances where we were unable to make satisfactory determinations, specific epithets have been omitted. Working at the Harvard University Herbaria (A and GH), D. E. Boufford and S. A. Spongberg took primary responsibility for the identifications of the expedition materials in the United States. T. R. Dudley provided determinations for *Ilex* and *Viburnum* and assisted with additional genera, while B. Bartholomew identified the specimens of *Camellia.* The assistance of L. Constance (Umbelliferae), K. Flinck (*Cotoneaster*), L. Garay (Orchidaceae), I. Hay (Gymnospermae), T. Koyama (Juncaceae, Cyperaceae), E. Landolt (*Lemna*), H. W. Li (certain Labiatae), E. McClintock (*Hydrangea*), P. O'Connor (Gramineae), P. H. Raven (*Epilobium*), and B. G. Schubert (*Begonia, Dioscorea,* and certain Leguminosae) is also gratefully acknowledged.

Primary responsibility for identifications in the People's Republic of China was assumed by Z. Cheng, at the Wuhan Institute of Botany, and Y. C. Tang and T. S. Ying, Institute of Botany, Beijing. R. C. Ching and K. H. Shing kindly studied the pteridophytes, while T. T. Yü, L. T. Lu, and T. C. Ku examined the specimens of Rosaceae, R. H. Shan examined the Umbelliferae, and A. L. Chang studied the Ericaceae.

Prior to the departure of the American participants from China, the herbarium material, as well as the germ-plasm collections, was divided equally between the Chinese and American teams. A complete set of the 1980 Sino-American Botanical Expedition specimens of vascular plants (1715 numbers) is at HIB, and the second most complete set (1695 numbers) is at A; specimens beyond these two sets were divided more or less equally between the institutions of the participants (CM, 1413 numbers; KUN, 1431; NA, 1441; NAS, 1466; NY, 1433; PE, 1605; SFDH, 1309; UC, 1489; and WH, 1199). Specimens in addition to the sets deposited in the institutions of the American participants have been sent as gifts to the Royal Botanic Garden, Edinburgh (E, 872 numbers), the Department of Botany, Kyoto University (KYO, 454 numbers), and the Missouri Botanical Garden (MO, 173 numbers). Unfortunately, a portion (approximately 200 sheets) of the herbarium specimens alloted to the American team inexplicably disappeared after their safe arrival in the United States and after the determinations had been completed, resulting in less complete sets than would have otherwise been possible.

In an attempt to make the following enumeration of greater value than a mere floristic listing, we have appended brief notes where we found taxonomic or nomenclatural problems during the identification process. It is hoped that these notes will stimulate further investigations that will ultimately help clarify problems in the systematics of these central Chinese plants. Acronyms of the herbaria (following Holmgren, Keuken, & Schofield, 1981, with the exception of the Shennongjia Forest District Herbarium, abbreviated SFDH) where the specimens are deposited are given for each collection number. Also, literature citations of original descriptions are provided for names not appearing in *Index Kewensis* or its *Supplements,* or in *Index Filicum* or its *Supplements.* APPENDIXES 1 and 2 provide a cross-reference to collection numbers and exact collecting localities, the elevation of each site, and the collection date. The collecting localities are indicated on MAP 2.

PTERIDOPHYTA[2]

LYCOPODIACEAE

Huperzia crispata (Ching) Ching, Acta Bot. Yunnanica **3:** 293. 1981. (syn.: *Lycopodium crispatum* Ching, Acta Phytotax. Sinica **18:** 236. 1980.)
1974 (A, HIB).

Huperzia hupehensis Ching*, Acta Bot. Yunnanica **3:** 301. 1981.
1386 (A, HIB, PE, UC).

Lycopodium obscurum L.
768 (A, HIB, NY, PE, UC).

SELAGINELLACEAE

Selaginella involvens (Sw.) Spring
624 (A, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1360* (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Selaginella labordei Hieron.
218 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *330* (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1080a* (A, NA, UC); *1593* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1691* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Selaginella moellendorffii Hieron.
1080 (A, HIB, KUN, NA, NAS, PE, SFDH, WH).

Collection no. *1080* represents a mixed collection, part of which (no. *1080a*) is *Selaginella labordei* Hieron. Some of the specimens cited here as *S. moellendorffii* in the Chinese herbaria may belong to that species.

Selaginella nipponica Makino
845 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Selaginella uncinata (Desv.) Spring*
1117 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

EQUISETACEAE

Equisetum arvense L.
1874 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Equisetum hyemale L.
141 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

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[2] The systematic arrangement of the families of Pteridophyta follows Ching (1978).

Equisetum ramosissimum Desf.
435 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

BOTRYCHIACEAE

Botrychium strictum Underw.
503 (HIB); *540* (HIB); *1686* (A, HIB, PE, UC).

HYMENOPHYLLACEAE

Hymenophyllum barbatum v. d. Bosch
2023 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

DENNSTAEDTIACEAE

Dennstaedtia pilosella (Hooker) Ching* (distributed as *Dennstaedtia hirsuta* (Hooker) Ching)
854 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Dennstaedtia wilfordii (Moore) Christ
563 (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC, WH); *1760* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Microlepia marginata (Houtt.) C. Chr.
2052 (A, HIB, NAS, PE, UC).

HYPOLEPIDACEAE

Hypolepis punctata (Thunb.) Mett.
1943 (A, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1944* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

LINDSAEACEAE

Stenoloma chusana (L.) Ching (syn.: *Sphenomeris chusana* (L.) Maxon)
2036 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

PTERIDACEAE

Pteridium revolutum (Blume) Nakai
674 (A, CM, E, HIB, KUN, KYO, NAS, NY, PE, SFDH, UC, WH); *1673* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Pteris excelsa Gaudich.*
1432 (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC); *1898* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Pteris nervosa Thunb.
495 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1654* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, WH).
Pteris vittata L.
1118 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1437* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Pteris wallichiana Agardh
2026 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

SINOPTERIDACEAE

Aleuritopteris duclouxii (Christ) Ching* (syn.: *Cheilanthes duclouxii* (Christ) Ching)
1674 (A, HIB, PE).
Aleuritopteris farinosa (Forsk.) Fée* (syn.: *Cheilanthes farinosa* (Forsk.) Kaulf.)
1754 (A, HIB).

Cheilsoria chusana (Hooker) Ching, comb. nov.
BASIONYM: *Cheilanthes chusana* Hooker, Sp. Fil. **2:** 95. *t. 106B.* 1852.
1600 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Leptolepidium kuhnii (Milde) Hsing & S. K. Wu*, Acta Bot. Yunnanica **1**(1): 117. 1979. (syn.: *Cheilanthes kuhnii* Milde)
1769 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Onychium ipii Ching*
1599 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Onychium japonicum (Thunb.) Kunze
2051 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Onychium moupinense Ching
545 (A, HIB).

ADIANTACEAE

Adiantum capillus-veneris L.
1915 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Adiantum davidii Franchet*
1357 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Adiantum edentulum Christ*
327 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *590* (A, CM, HIB, KUN, NA, NY, PE, SFDH, UC); *1767* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Adiantum erythrochlamys Diels*
326 (A, HIB, PE, UC); *497* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1712* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Adiantum myriosorum Baker
552 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Adiantum pedatum L.
1295 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1755* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1819* (A, HIB).

HEMIONITIDACEAE (GYMNOGRAMMACEAE)

Coniogramme caudiformis Ching & Shing*, Acta Bot. Yunnanica **3:** 233. 1981. (distributed as *Coniogramme caudifrons* Ching)
496 (A, HIB, NA, NAS, PE, UC); *1435* (A, CM, HIB, NA, NAS, PE, UC).
Coniogramme intermedia Hieron.
504 (A, HIB, NAS, PE, UC); *1446* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Coniogramme robusta Christ (distributed as var. *repandula* Ching, apparently an unpublished name)
2049 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

ATHYRIACEAE

Allantodia okudairai (Makino) Ching*, Acta Phytotax. Sinica **9:** 49. 1964.
1711 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Allantodia squamifera (Mett.) Ching*, Acta Phytotax. Sinica **9:** 55. 1964.
321 (A, CM, HIB, NAS, PE, UC); *1237* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Athyrium amplissimum Ching, Boufford, & Shing, sp. nov.

Species proxime affinis Athyrium multifido Rosenst., Japoniae, sed in statura multo majore, stipite virescente (nec purpurascente), pinnis pinnulisive multo majoribus, et pinnis breviter petiolatis differt.

Plants ca. 80 cm tall. Rhizome short, erect. Stipe ca. 35–40 cm long, 4 mm in diameter, stramineous, glabrous above base, which is covered with light brown, lanceolate scales; lamina ample, 40–45 cm long, to 40 cm wide, ovate, acuminate at apex, broadly rounded at base, tripinnate; pinnae ca. 13 pairs, lower ones nearly opposite but becoming alternate upward, rather closely spaced, sessile, oblong-lanceolate, acuminate to truncate base, subsessile, the basal pair nearly as large as those next above, ca. 20 cm long, 8–9 cm wide above narrowed base, bipinnate; pinnules ca. 25 pairs, spreading at right angles to rachis, sessile, lanceolate, acuminate at apex, subrounded at base, the longest ones 4 by 1.2 cm, the basal pair much reduced, ca. 1.2 cm long, pinnate; ultimate segments up to 15 pairs, oblong, 6 by 1.6 mm, with few teeth along margin. Fronds herbaceous, drying green, rachis and rachilets glabrous. Sori large, subrounded to oblong, 3 to 5 per segment, close; indusium small, fugaceous.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), vicinity of Dalongtan and Xiaolongtan on the W side of the road, elevation 2300–2600 m, 9 September 1980, *Sino-Amer. Bot. Exped. 914* (holotype, PE; isotypes, A, CM, E, HIB, KUN, KYO, NA, NAS, NY, SFDH, UC, WH).

ADDITIONAL SPECIMENS EXAMINED. **China.** HUBEI: Shennongjia Forest District (31° 30′N, 110°30′E), mixed deciduous-coniferous-bamboo forest remnant at Chuifeng Pass, ca. 3000 m, fronds tufted from erect rhizomes, *1980 Sino-Amer. Bot. Exped. 49* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); vic. of Xiaojiuhu, ca. 2000 m, semiopen, moist slope in *Quercus* forest, fronds tufted from erect rhizomes, stipes green or brownish, *1980 Sino-Amer. Bot. Exped. 1348* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Somewhat similar to *Athyrium multifidum* Rosenst., but differing in being much larger and in having green (not purplish) stipes, much larger pinnae and pinnules, and pinnae with shorter petioles.

Athyrium epirachis (Christ) Ching
2011 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Athyrium fallaciosum Milde*
1768 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Athyrium filix-femina (L.) Roth.*
351 (A, CM, HIB, KUN, NA, NAS, PE, UC).
Athyrium mackinnoii (Hope) C. Chr.*
320 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Athyrium vidalii (Franchet & Sav.) Nakai*
333 (A, HIB, KUN, PE, UC); *2053* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Athyrium wardii (Hooker) Makino*
542 (A, HIB, KUN, NAS, PE, UC).
Athyrium sp. (distributed as *A. deflexum* Ching, apparently an unpublished name)
1876 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Dryoathyrium dielsii (C. Chr.) Ching*
544 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1091* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Dryoathyrium henryi (Baker) Ching
588 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC); *620* (HIB); *621* (HIB); *1000* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Dryoathyrium okuboanum (Makino) Ching*, Acta Phytotax. Sinica **10:** 303. 1965.
706 (A, HIB, KUN, NA, NY, PE, UC).
Dryoathyrium unifurcatum (Baker) Ching*
1434 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Lunathyrium shennongense Ching, Boufford, & Shing, sp. nov.

Species insignis, adspectu Lunathyrium vermiformi Ching, Boufford, & Shing proxime affinis, sed in stipite rachidique subtus glabris supra in sulco pilis minutis septatis sparsis praedito, costis pinnarum subtus similiter sparse villosis, segmentis angustioribus, sinubus latis, indusiis brevioribus latioribusque subconchatis cinereis membranaceis marginibus erosis (indusiis in pinnis supremis plerumque hippocrepiformibus), differt.

Plants to 70 cm tall. Stipe 12 cm long, 2.2 mm in diameter, pale-stramineous, bisulcate on upper side, scaly at base, glabrous upward; lamina oblanceolate, to 60 cm long, 15 cm wide at middle, acuminate at apex, gradually narrowed toward base, which is ca. 5 cm wide; pinnae ca. 22 pairs, patent, the lower ones separated by broad intervals, the basal pair 3–4 cm long, somewhat deflexed, the middle ones 10 cm long, 1.8 cm wide at base, sessile or subsessile, lanceolate, acuminate at apex, truncate at base, pinnatipartite; segments ca. 22 pairs, spreading at right angles to costa, ca. 7 mm long, 3 mm wide at base, oblong, obtuse at apex, entire; veins 6 or 7 pairs in each segment, simple. Fronds drying green, glabrous except for costa on undersurface of pinnae, which has few fine, septate hairs, these more

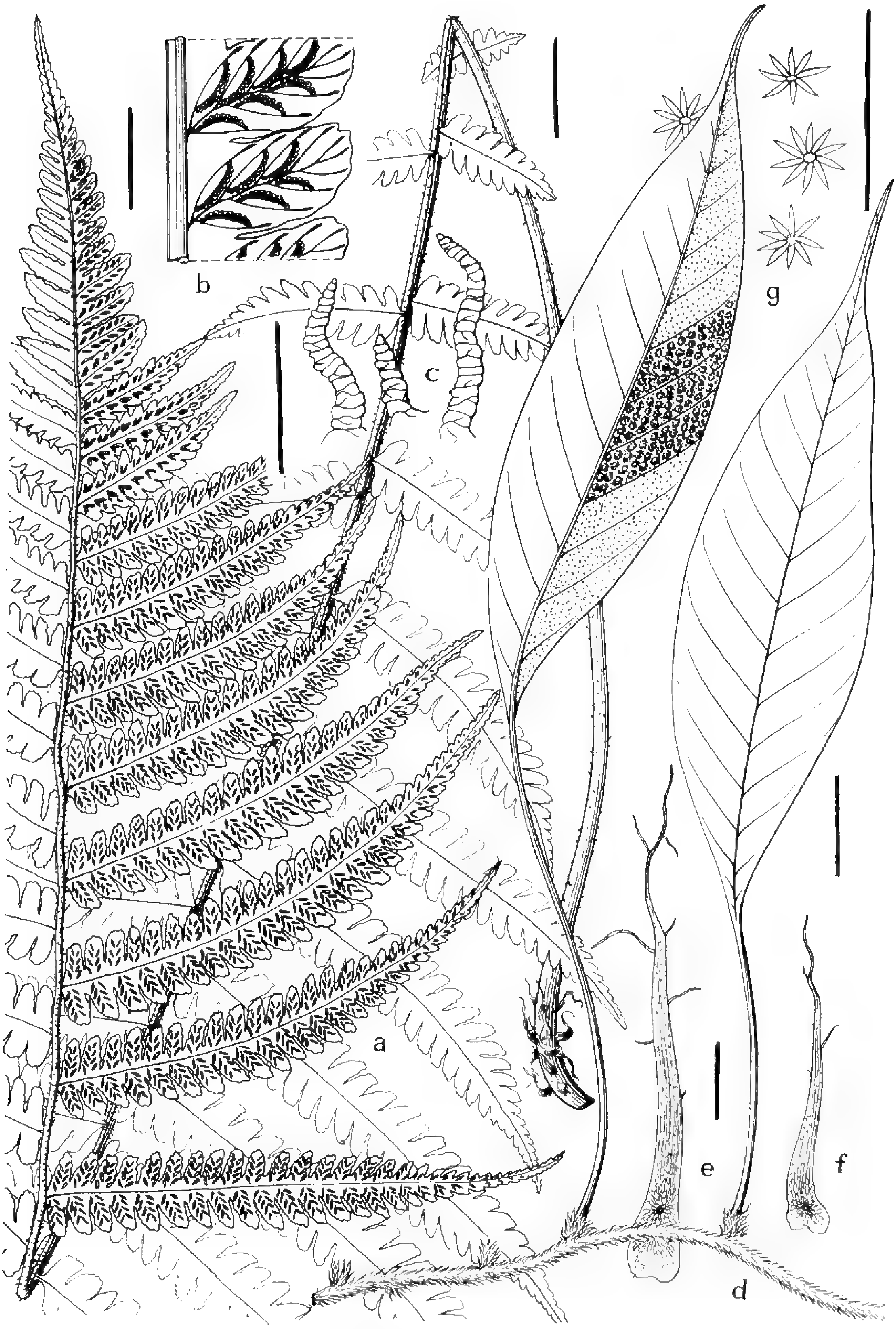

FIGURE 7. a–c, *Lunathyrium vermiforme:* a, frond (bar = 2 cm); b, portion of pinna with sori (bar = 5 mm); c, setae from rachis (bar = 1 mm). d–g, *Pyrrosia caudifrons:* d, fronds and rhizome (bar = 2 cm); e, f, scales from rhizome (bar = 1 mm); g, stellate hairs from undersurface of lamina (bar = 1 mm).

dense on upper surface of rachis. Sori oblong, contiguous, 4 or 5 pairs per segment; indusium subconchoidal (those on uppermost pinnae generally horseshoe shaped), gray, membranous, margin erose.

Type. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), vicinity of Chuifeng Pass, elevation ca. 2700 m; openings in bamboo thickets, fronds with erect rhizomes, 26 August 1980, *Sino-Amer. Bot. Exped. 353* (holotype, PE; isotypes, A, CM, HIB, KUN, KYO, NA, NAS, NY, SFDH, UC, WH).

Although *Lunathyrium shennongense* resembles *L. vermiforme* Ching, Boufford, & Shing morphologically, it differs in having a stipe and rachis that are glabrous beneath and sparsely hairy with fine, septate hairs in the groove on the upper side (the costa on the undersurface of the pinnae also has a few similar hairs), segments that are narrower with broader sinuses, and short, broad, subconchoidal, membranous, ash-gray indusia with erose margins.

Lunathyrium vermiforme Ching, Boufford, & Shing, sp. nov. Figure 7, a–c.

Species e turma Lunathyrium giraldii (Christ) Ching, sed in pinnis inferioribus minus abbreviatus, rachidibus omnino setis crassis vermiformibus copice praeditis, pinnis majoribus, differt.

Plants to 74 cm tall. Rhizome short, erect; fronds fasciculate. Stipe ca. 20 cm long, 2 mm in diameter, dark-stramineous, glabrous above base, which is covered with dark brown. lanceolate scales; lamina elliptic-lanceolate, 55 cm long, 18 cm wide at middle, acuminate at apex, gradually narrowed toward base, bipinnatipartite; pinnae ca. 20 pairs, patent, separated by narrow intervals, the lower widely separated, the lowest 4 pairs abbreviated, the basal pair auriculate, ca. 1 cm long, the middle ones to 10 cm long, 1.6 cm wide at truncate base, lanceolate, slightly falcate, acuminate at apex, pinnatipartite to narrow wing along costa; segments ca. 20 pairs, close, oblong, ca. 7 by 4 mm, entire, apex obliquely truncate or subrounded. Fronds herbaceous, drying green, pinnae glabrous on both sides, rachis covered throughout with thick, pale setae. Sori linear, extending from midrib to near margin, indusia linear, entire, straight throughout, well spaced.

Type. China, western Hubei Province, metasequoia region of Lichuan Xian (30°10′N, 108°45′E), vicinity of Zhuanjiaowan on the E side of the valley, elevation ca. 1500 m, 7 October 1980, *Sino-Amer. Bot. Exped. 2025* (holotype, PE; isotypes, A, CM, HIB, KUN, KYO, NA, NAS, NY, SFDH, UC, WH).

Lunathyrium vermiforme is related to *L. giraldii* (Christ) Ching of the same region but differs in having larger pinnae, with the lower ones less abbreviated, and the rachis covered throughout with numerous thick setae.

Lunathyrium wilsonii (Christ) Ching, Acta Phytotax. Sinica **9:** 71. 1964.
2048 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Lunathyrium sp. (mistakenly identified and distributed as *Lunathyrium centrochinense* Ching)
1239 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Pseudocystopteris atkinsonii (Bedd.) Ching, Acta Phytotax. Sinica **9:** 78. 1964.
322 (A, HIB, UC); *909* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1238* (A, HIB, UC).
Pseudocystopteris longipes (Christ) Ching*, Acta Phytotax. Sinica **9:** 78. 1964.
46 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *873* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

THELYPTERIDACEAE

Cyclosorus acuminatus (Houtt.) Nakai (syn.: *Thelypteris acuminata* (Houtt.) Morton)
1104 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Macrothelypteris oligophlebia (Baker) Ching, Acta Phytotax. Sinica **8:** 309. 1963, var. *elegans* (Koidz.) Ching, *ibid.*
1436 (A, HIB, NA, PE, UC).
Parathelypteris nipponica (Franchet & Sav.) Ching, Acta Phytotax. Sinica **8:** 302. 1963. (syn.: *Thelypteris nipponica* (Franchet & Sav.) Ching)
306 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Phegopteris decursive-pinnata (Van Hall) Fée (syn.: *Thelypteris decursive-pinnata* (Van Hall) Ching)
246 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1433* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *2047* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Phegopteris polypodioides Fée* (syn.: *Thelypteris phegopteris* (L.) Slosson ex Rydb.)
913 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Pronephrium penangiana (Hooker) Holttum (syn.: *Abacopteris penangiana* (Hooker) Ching)
492 (A, CM, HIB, KUN, NAS, PE, UC); *1116* (A, HIB, NAS, NY, PE, UC).
Pseudophegopteris pyrrorachis (Kunze) Ching*, Acta Phytotax. Sinica **8:** 315. 1963.
758 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Thelypteris subocthodes (Ching) Ching* (distributed as *Pseudocyclosorus tsoi* Ching)
1946 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

ASPLENIACEAE

Asplenium incisum Thunb.
1692 (HIB).
Asplenium sarelii Hooker
328 (A, HIB); *430* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Asplenium trichomanes L.
760 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1448* (A, HIB, UC).

No. *760* was distributed as *Asplenium trichomanes* L. subsp. *orientale* Lovis.

Asplenium tripteropus Nakai
2046 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Asplenium unilaterale Lam.
1920 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

PLEUROSORIOPSIDACEAE

Pleurosoriopsis makinoii (Maxim.) Fomin*
1296 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

ONOCLEACEAE

Matteuccia intermedia C. Chr.
23 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Matteuccia orientalis (Hooker) Trev.
720a (A, CM, NA, UC); *1890* (A, HIB); *2050* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Collection no. *720* originally represented a mixed collection and was divided into two parts, *720* and *720a.* Other than for the specimen serving as the holotype of *Matteuccia orientalis* f. *monstra* (distributed as *Matteuccia centro-chinense,* an unpublished name), the identity and disposition of these two numbers in Chinese herbaria are not known. However, specimens were deposited in HIB, KUN, NAS, SFDH, and WH under no. *720.*

Matteuccia orientalis (Hooker) Trev. forma **monstra** Ching & Shing, forma nov. FIGURE 8.

A forma typica differt pinnis lateralibus angustioribus integrisque infra partem apicalem plus minusve incisas.

Sterile fronds ca. 80 cm tall. Stipe to 30 cm long, 6 mm in diameter, stramineous, densely covered at base with lanceolate, light brown, entire scales ca. 1.6 cm long, subglabrous upward; lamina oblong, ca. 50 by 34 cm, imparipinnate; pinnae ca. 20 pairs, obliquely patent, opposite, the lower ones separated by intervals ca. 2–3 cm wide, becoming closer upward, the basal pinnae as long as those above, to 17 by 1.5 cm, narrower (ca. 7 mm) toward base, subsessile, linear, acuminate, margins crenate, the upper pinnae similar but with apical portion pinnatifid with segments ca. 6 mm long; veins in all segments simply forked. Fronds glabrous, drying brownish green. The fertile fronds ca. 60 cm tall; stipe 35 cm long, dark-stramineous, glabrous above base; lamina 28 cm long; fertile pinnae approximate, sessile, linear, dark brown, glossy, leathery, distichous, 6 by 4 mm, reflexed margin persistently incurved, indusium brownish, fimbriate.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′W), vicinity of Muyuping Forest Brigade on the SE side of the watershed divide between the Changjiang (Yangtze) and Hanjiang rivers near km 73 from Xingshan Xian, elevation 1450–1600 m; cutover *Fagus-Quercus-Bet-*

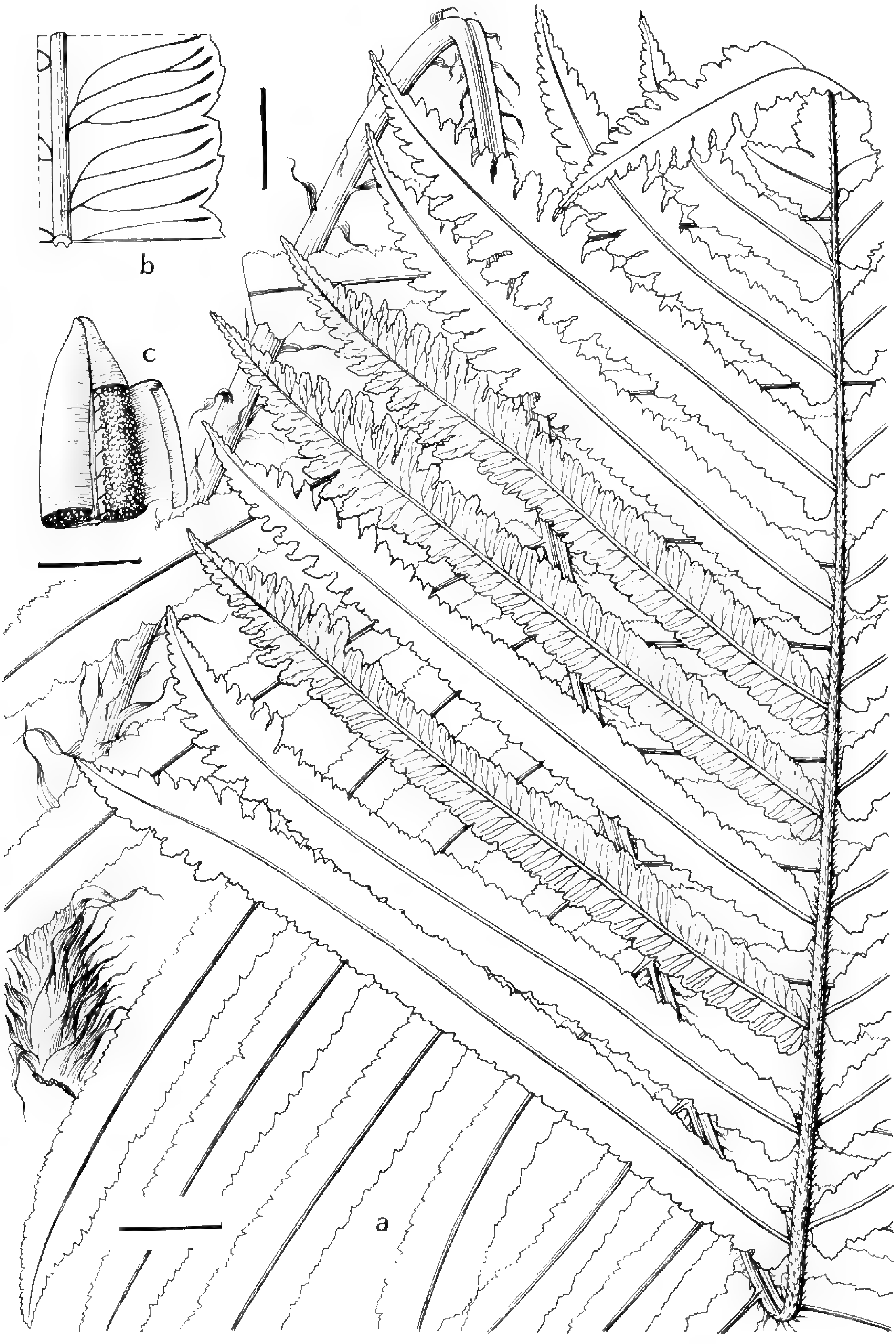

FIGURE 8. *Matteuccia orientalis* f. *monstra:* a, sterile frond (bar = 2 cm); b, portion of sterile pinna (bar = 5 mm); c, apical portion of fertile pinna (bar = 5 mm).

ula forest on steep, moist slopes, SE exposure; fronds tufted from erect rhizome, 7 September 1980, *Sino-Amer. Bot. Exped. 720* (holotype, PE; isotypes, A, NY).

A peculiar form differing from all other known members of the genus in having sterile fronds with narrowly linear, crenate pinnae (the upper ones pinnatifid apically) and simply forked veins. This may be an abnormal form of *Matteuccia orientalis* (Hooker) Trev.; further field observations are needed.

Matteuccia struthiopteris (L.) Todaro*
999 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

WOODSIACEAE

Woodsia polystichoides D. C. Eaton
853 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

BLECHNACEAE

Struthiopteris eburnea (Christ) Ching* (syn.: *Blechnum eburneum* Christ)
1896 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Woodwardia unigemmata (Makino) Nakai
486 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *2057* (A, HIB, UC).

PERANEMACEAE

Peranema cyathioides D. Don
2085 (A, HIB).

DRYOPTERIDACEAE

Cyrtomium fortunei J. Sm.
238 (A, HIB); *1500* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1569* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Cyrtomium macrophyllum Tagawa
238a (A); *1092* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Dryopteris apicifixa Ching, Boufford, & Shing, sp. nov.

Species proxime affinis Dryopteris juxtaposita Christ, sed in statura multo minore, rachi paleacea, pinnis pinnulisque multo brevioribus, soris ad pinnis supremas restrictis, differt.

Plants ca. 50 cm tall. Rhizome short, erect; fronds tufted. Stipe ca. 23 cm long, 1.2 mm in diameter, stramineous, densely covered at base with broadly lanceolate, thin, light brown scales; lamina oblong, 28 cm long, 15 cm wide at base, acuminate at apex, bipinnate; pinnae pinnate, ca. 6 pairs, opposite, short-petiolate, patent, the basal pair slightly larger, 9 by 4 cm, oblong, acuminate at apex, rounded at base, the upper ones similar in outline but gradually smaller than basal pair; pinnules ca. 10 pairs, closely spaced, basiscopic ones longer than acroscopic, the basal one not abbreviated, as large as those upward, 2–3 cm long, 1 cm wide at base, sessile, lanceolate, acute at apex, pinnatifid with few rounded lobes, the acroscopic pinnules 1.5 cm long, 8 mm wide at base, oblong, blunt at apex, margins crenate. Fronds drying light green, glabrous except for rachis, which is covered with rather sparse, lanceolate, dark brown scales. Sori small, confined to apical part of lamina, 2 or 3 pairs per pinnule; indusium light brown, rather thin, curling, deciduous.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), along the trail between Hongriwan construction camp and Quijiaping, elevation 1200–1400 m; growing in bamboo thicket, 2 September 1980, *Sino-Amer. Bot. Exped. 543* (holotype, PE; isotypes, A, CM, HIB, UC).

Dryopteris apicifixa is related to *D. juxtaposita* Christ but differs in its much smaller size, its scaly rachis, its much shorter pinnae, and its pinnules with the sori confined to the apical part of the lamina.

Dryopteris bissetiana (Baker) C. Chr.*
849 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Dryopteris handelii C. Chr.*
1293 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Dryopteris infrapuberula Ching, Boufford, & Shing, sp. nov. FIGURE 9.

Species insignis habitu Dryopteris yunnanensis Christ e provincia Yunnan, sed in stipite (e basi sursum) omnino glabro, pinnis ad basin conspicue dilatatis, venis in segmentis omnibus simplicibus, et pinnis subtus praecipue secus venas sparse puberulis, facile distinguitur.

Plants ca. 80 cm tall; growing tip covered with dark brown, broadly lanceolate scales; fronds tufted. Stipe ca. 23 cm long, 3 mm in diameter, dark straw colored, nearly glabrous from base upward; lamina elliptic-oblong, 40 cm long, 23 cm wide at middle, acuminate at apex, slightly narrowed toward base, pinnate-pinnatilobed; pinnae ca. 23 pairs, patent, separated by narrow intervals, the basal pair somewhat abbreviated, to 7 cm long, horizontally patent, the middle ones to 13 cm long, 2 cm wide at base, sessile, lanceolate, acuminate at apex, dilated at base, lobate-pinnatifid, with lobes ca. 3 by 5 mm, roundish, entire; veins 5 pairs in each lobe, simple, anterior basal vein reaching sinus, posterior one reaching margin slightly above sinus. Fronds chartaceous, drying green, the rachis copiously covered with dark brown, linear, appressed scales, the undersurfaces of costae covered with small, lanceolate, brown scales with ciliate margins, the midribs and veins with few minute hairs. Sori rather small, 3 or 4 pairs per segment, medial; indusium dark brown, firm, ultimately deciduous.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), vicinity of Quijiaping, elevation 1440–1650 m; moist, level areas along stream in mixed deciduous–broad-leaved evergreen–coniferous forest, 3 September 1980, *Sino-Amer. Bot. Exped. 619* (holotype, PE; isotypes, A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

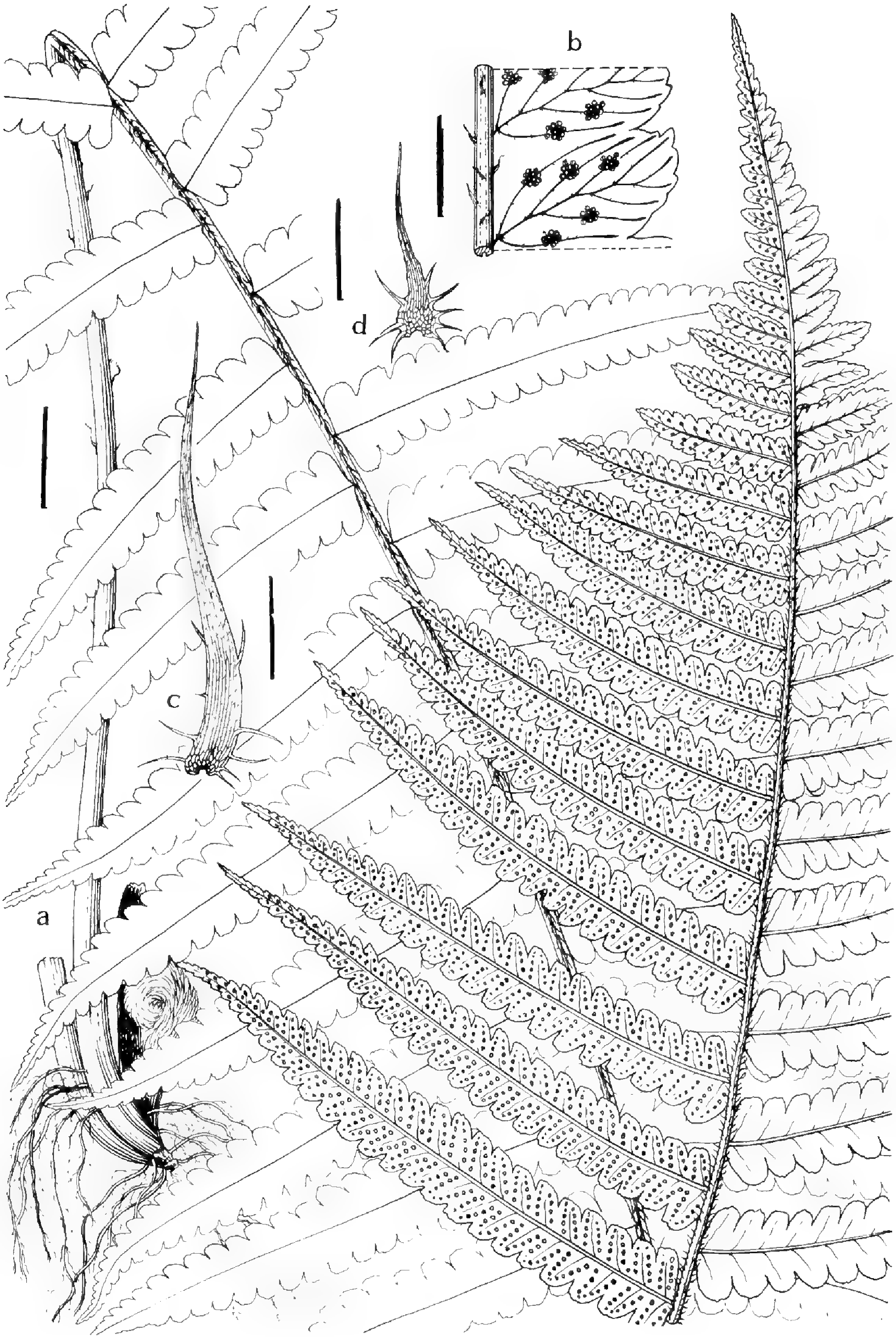

FIGURE 9. *Dryopteris infrapuberula:* a, frond (bar = 2 cm); b, portion of pinna with sori (bar = 5 mm); c, scale from undersurface of rachis (bar = 1 mm); d, scale from undersurface of costa (bar = 1 mm).

Dryopteris infrapuberula is an outstanding species of the group containing *D. yunnanensis* Christ, from Yunnan Province, but is easily distinguished by the dark straw colored stipe naked from the base upward, the pinnae with broadened bases, the veins in the segments all simple, and the undersurfaces of the pinnae (especially along the veins) sparsely puberulous.

Dryopteris labordei (Christ) C. Chr.
2054 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Dryopteris nemagetae (Kurata) Kurata*
1292 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Dryopteris neolacera Ching*
759 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).
Dryopteris rosthornii (Diels) C. Chr.
311 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Dryopteris submarginalis Ching, Boufford, & Shing, sp. nov. FIGURE 10.

Species ex affinitate Dryopteris pulcherrimae Ching, sed in statura multo majore (planta usque ad 78 cm alta), lamina latiore, pinnis longioribus, costis subtus distincte canaliculatis, et soris submarginalibus, recedit.

Plants to 78 cm tall; rhizome short, erect; fronds fasciculate. Stipe short, to 10 cm long, 5 mm in diameter, densely covered with dark brown, lanceolate scales; lamina to 68 cm long, 16 cm wide at middle, oblanceolate, acuminate at apex, gradually narrowed toward base, base ca. 8 cm wide, bipinnatipartite; pinnae numerous, ca. 38 pairs, patent, sessile, separated by narrow intervals, lower ones more widely separated, the basal pair 4 cm long, the middle ones to 8 cm long, 1.5 cm wide at base, lanceolate, acuminate at apex, truncate at base, pinnatipartite to narrow wing along each side of costa; segments ca. 22 pairs, patent, separated by narrow sinuses, oblong, ca. 6 by 2 mm, entire; veins 5 or 6 pairs in each segment, simple, oblique. Fronds herbaceous, drying green, costa canaliculate beneath, copiously covered with brown, ovate, membranaceous scales, glabrous above except for some brown, deciduous fibrils along lower part of costa; rachis densely covered beneath with ovate-acuminate, fimbriate scales, densely fibrillose above. Sori rather small, 3 to 5 pairs per segment, submarginal; indusium light brown, firm, ultimately curling, usually persistent.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), S end of the Loyang River gorge near Pingqian, elevation ca. 1300 m; deciduous forest on steep slope along the river, 14 September 1980, *Sino-Amer. Bot. Exped. 1356* (holotype, PE; isotypes, A, CM, HIB, KUN, KYO, NA, NAS, NY, SFDH, UC, WH).

Dryopteris submarginalis is related to *D. pulcherrima* Ching of the same region, but differs in its much larger size, its broader lamina and longer pinnae, and its costae that are distinctly canaliculate beneath.

Dryopteris supraimpressa Ching, Boufford, & Shing, sp. nov.

Species affinis Dryopteris marginatae (Hope) Christ, sed in statura multo minore, lamina basi tripinnatifida nec tripinnata, pinnulis brevioribus api-

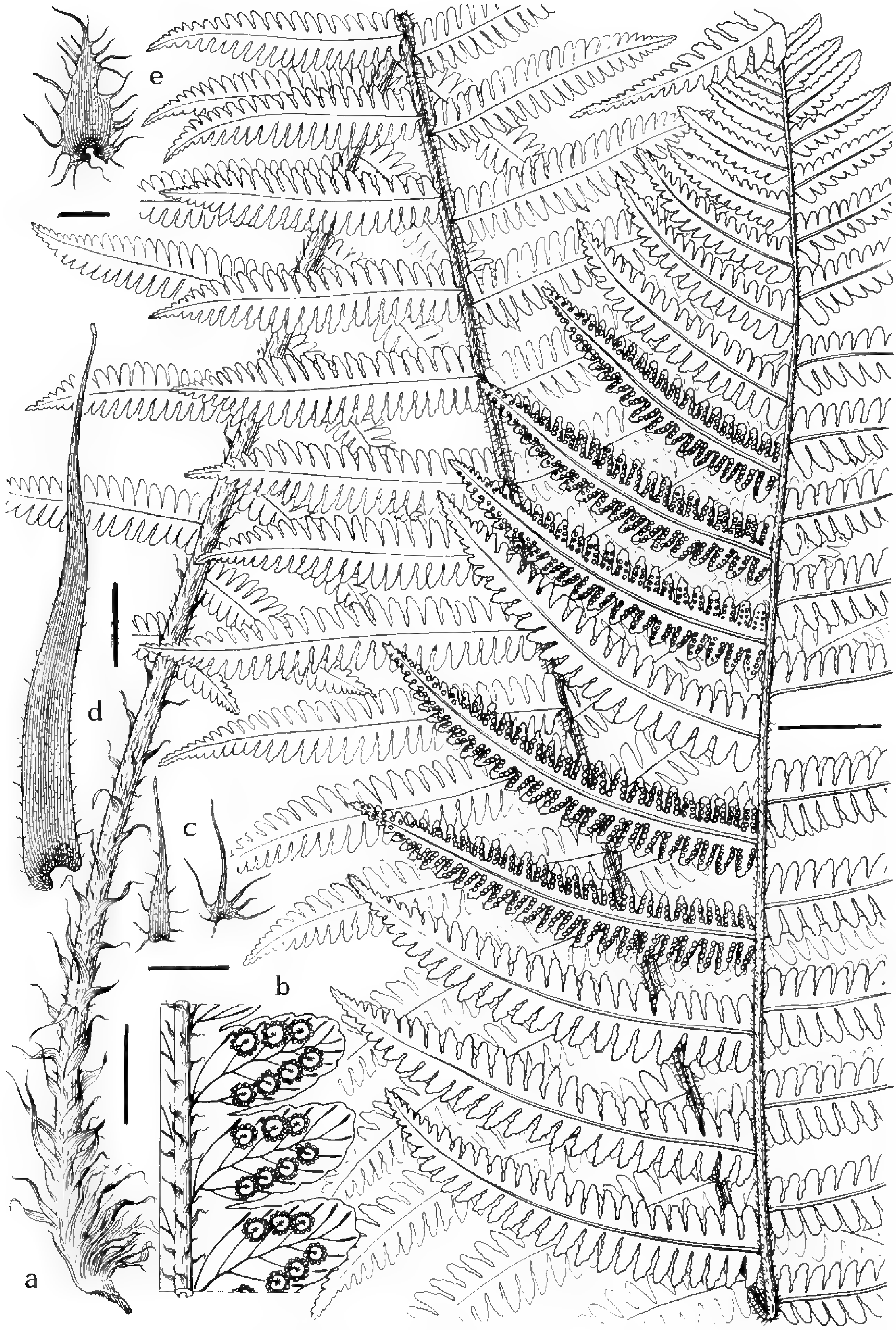

FIGURE 10. *Dryopteris submarginalis:* a, frond (bar = 2 cm); b, portion of pinna with sori (bar = 5 mm); c, d, scales from stipe (bars = 2 mm); e, scale from rachis (bar = 1 mm).

cibus obtusiusculus, firme chartaceis, et venis supra distincte impressis apice hydathodo impresso rotundo prope marginem terminatis, differt.

Plants to 75 cm tall. Stipe 26 cm long, 3 mm in diameter, stramineous, covered at base with brown, lanceolate scales ca. 1 cm long, glabrous upward; lamina ovate, ca. 50 by 34 cm, acuminate at apex, rounded at base, pinnate-pinnatifid; pinnae ca. 10 pairs, close, obliquely patent, petiolate, the basal pair as large as those next above, ca. 20 by 9 cm, oblong-lanceolate, pinnate, acuminate at apex, truncate at base, petiole ca. 1 cm long; pinnules ca. 13 pairs, smaller upward, spreading, closely spaced, sessile, the basioscopic ones slightly longer than acroscopic ones, the basal pinnule not abbreviated but as long as the next 2 on same side, ca. 6 cm long, 1.2 cm wide at base, lanceolate, slightly falcate, apex acute, pinnatifid from slightly over halfway to base, obtusely lobed, the acroscopic pinnules ca. 4 cm long, apex obtuse, margins lobed or crenate; veins distinctly impressed above, ending in round, impressed hydathode near margin. Fronds thick-chartaceous, drying green, both surfaces and rachis glabrous. Sori medium sized, 4 to 7 (or 8) pairs per pinnule, near midrib; indusium light brown, firm, curling at maturity, ultimately deciduous.

TYPE. China, western Hubei Province, metasequoia region of Lichuan Xian (30°10′N, 108°45′E), vicinity of Zhuanjiowan on the E side of the valley, elevation ca. 1500 m, 7 October 1980, *Sino-Amer. Bot. Exped. 2020* (holotype, PE; isotypes, A, CM, HIB, KUN, NA, NAS, NY, UC).

Dryopteris supraimpressa is a distinct species of the group containing *D. marginata* (Hope) Christ. It differs from *D. marginata* in its smaller size, its thick-chartaceous texture, and its distinctly impressed nerves terminated by round, impressed hydathodes near the margin on the upper surface of the pinnules.

Dryopteris tokyoensis (Makino) C. Chr.*
1258 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Polystichum craspedosorum (Maxim.) Diels
418 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Polystichum deltodon (Baker) Diels
500 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1079* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Polystichum erosum Ching & Shing*, Acta Phytotax. Sinica **10:** 303. 1965.
1764 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC).

Polystichum lobatopinnulum Ching, Boufford, & Shing, sp. nov.

Habitu Polystichum makinoii Tagawa similis, sed in pinnulis minoribus, margine inferiore aristis fere destitutis, pinnula basali acroscopica quam ceteris longiore margine lobato-incisa et sori submarginalibus recedit.

Plants to 57 cm tall. Stipe to 20 cm long, 2.5 mm thick, pale-stramineous, the lower part covered with large, ovate-acuminate, brown as well as blackish scales, the scales on upper part of stipe smaller, brown, lanceolate, with long, hair-tipped apex; lamina narrowly oblong to broadly lanceolate, ca. 40 by 11 cm, acuminate at apex, not narrowed at base, bipinnate; pinnae ca. 20 pairs, sessile, lanceolate, ca. 5.5 cm long, 1.6 cm wide above truncate base, acuminate at apex, produced on anterior side, separated by narrow intervals; pinnules ca. 12 pairs, patent, oblong, subfalcate, ca. 7 by 3.5 mm, acute at apex, with deltoid auricle at anterior base, margins more or less aristate-serrate, the acroscopic basal pinnule longer than others, 1.2 cm long, lobate-incised. Fronds herbaceous when dry, greenish, glabrous above, sparsely fibrillose on costules beneath, rachis densely covered with brown, lanceolate, deflexed scales, these subulate at apex. Sori small, submarginal; indusium dark brown, firm, ultimately deciduous.

TYPE. China, western Hubei Province, metasequoia region of Lichuan Xian (30°10′N, 108°45′E), vicinity of Zhuanjiaowan on the E side of the valley, elevation ca. 1500 m; moist, steep, rocky slope, 7 October 1980, *Sino-Amer. Bot. Exped. 2059* (holotype, PE; isotypes, A, CM, HIB, KUN, KYO, NA, NAS, NY, SFDH, UC, WH).

Polystichum lobatopinnulum is similar to *P. makinoii* Tagawa in habit, but differs in the smaller pinnules with the lower margins nearly without aristate teeth, the longer and lobate-incised acroscopic basal pinnule, and the submarginal sori.

Polystichum longiaristatum Ching, Boufford, & Shing, sp. nov.

Species arcte affinis Polystichum shennongense Ching, Boufford, & Shing, sed in stature minore, stipite paleis minoribus sparsioribus obtecto, pinnis minoribus infimis quam sesquentibus paulo longioribus, pinnula basali acroscopica paulo elongata sed integra, et pinnulis apicibus acutis et marginibus longius aristato-serrulatis, differt.

Plants ca. 70 cm tall. Stipe ca. 22 cm long, 2 mm in diameter, pale-stramineous, moderately covered with broad, brown scales (lower ones darker); lamina narrowly oblong, ca. 42 cm long, 16 cm wide at middle, 19 cm wide at base, bipinnate; pinnae ca. 23 pairs, patent, separated by narrow intervals, the basal pair longer than those next above, ca. 9 cm long, 2 cm wide above base, lanceolate, acuminate at apex, pinnate; pinnules ca. 15 pairs, patent, closely spaced, the apex acute, the base cuneate, with acroscopic, deltoid auricle, the margins scarcely serrate but with very long, fine aristae. Fronds chartaceous, drying green; undersides, costae, and rachis with dense, brown, linear-lanceolate, hair-tipped, deflexed scales; pinnules glabrous above, with few brown fibrils beneath. Sori small, 4 or 5 pairs per pinnule, medial; indusium small, fugaceous.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), Zhushanyazi Pass on the W side of the Dajiuhu basin, elevation ca. 1780 m; moist ravines and stream margins in *Quercus-Fagus-Populus* forest on low hills, 13 September 1980, *Sino-Amer. Bot. Exped. 1248* (holotype, PE; isotypes, A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, SFDH, UC, WH).

Polystichum longiaristatum is closely related to *P. shennongense* Ching, Boufford, & Shing, from which it differs in its smaller size, its stipes covered with smaller and less dense scales, its pinnae with a somewhat elongate, entire, anterior basal pinnule, and its pinnules all with acute apices and less prominently serrate margins, but with much longer, weaker aristae.

Polystichum neolobatum Nakai
541 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1228* (A, CM, HIB, KUN, NA, NAS, NY, PE, UC); *1818* (A, HIB).
Polystichum pteroptrum (Maxim.) Diels*
1235 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Polystichum shennongense Ching, Boufford, & Shing, sp. nov. FIGURE 11.

Species adspectu arcte affinis Polystichum longiaristati Ching, Boufford, & Shing, sed in stipite paleis majoribus densioribusque obtecto, pinnis basalibus unijugis quam sequentibus brevioribus, pinnis mediis basi antica pinnula elongata pinnatifida praeditis et pinnulis apicibus acutis vel subobtusis, marginibus aristis brevioribus armatis, recedit.

Plants to 1 m tall. Stipe ca. 30 cm long, 5–6 mm in diameter, very densely covered with large, ovate-acuminate, light brown, spreading scales; lamina ca. 70 by 24 cm, elongate-oblong, acuminate at apex, slightly narrowed at base, bipinnate; pinnae ca. 30 pairs, spreading, sessile, alternate, separated by intervals equal in width to pinnae, or lower ones opposite with intervals wider than pinnae, the basal pinnae 8–9 cm long, the middle pinnae 12–13 cm long, 2 cm wide above base, linear, acuminate at apex, truncate at base, oblique, pinnate; pinnules ca. 19 pairs, close, patent, oblong, 1 by 6 mm, straight below, with deltoid auricle above, acute or subobtuse at apex, margins aristate-serrate, the anterior basal pinnule elongate, 1.5 cm long, pinnatifid, close to rachis. Fronds thinly chartaceous, drying green, both sides sparsely fibrillose, costa of pinnae scaly beneath, rachis densely covered with light brown, broadly lanceolate, hair-tipped, reflexed scales. Sori small, 4 or 5 pairs per pinnule, medial; indusium rufous brown, firm, persistent.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), Zhushanyazi Pass on the W side of the Dajiuhu basin, elevation ca. 1780 m; *Quercus-Fagus-Populus* forest on low hills, along stream bed in shade, 13 September 1980, *Sino-Amer. Bot. Exped. 1236* (holotype, PE; isotypes, A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, SFDH, UC, WH).

Although *Polystichum shennongense* closely resembles *P. longiaristatum* Ching, Boufford, & Shing in general habit, it differs in having the stipes covered in larger and denser scales, the basal pair of pinnae not larger than those next above, the middle pinnae with an elongate, pinnatifid pinnule on the anterior base, and the pinnules with a subobtuse or acute apex and shortly aristate-serrate margins.

Polystichum submite (Christ) Diels*
325 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

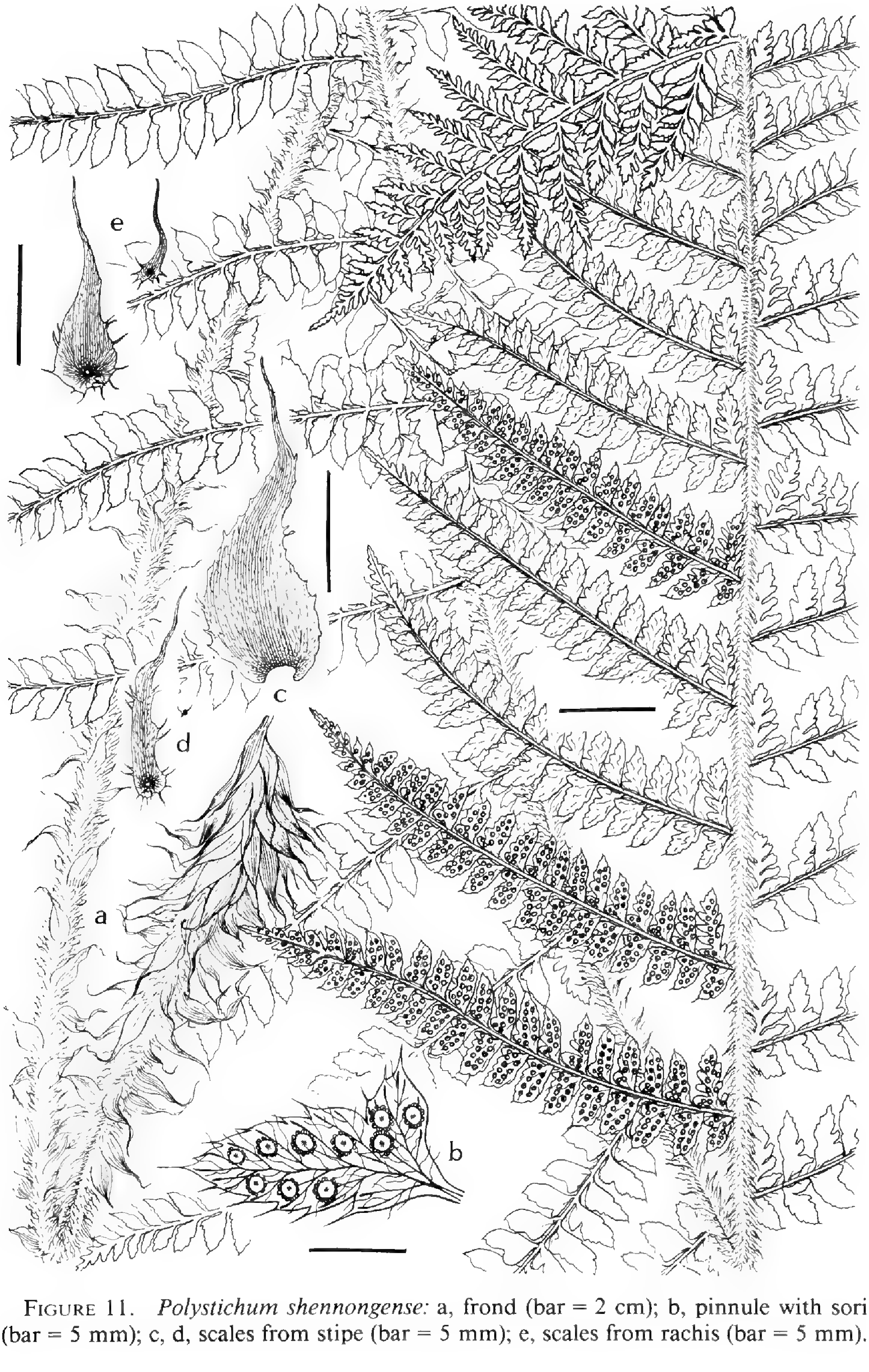

FIGURE 11. *Polystichum shennongense:* a, frond (bar = 2 cm); b, pinnule with sori (bar = 5 mm); c, d, scales from stipe (bar = 5 mm); e, scales from rachis (bar = 5 mm).

Polystichum tsus-simense (Hooker) Moore
  406 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1062* (A, CM, HIB, KUN, NAS, NY, PE, UC); *1653* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

POLYPODIACEAE

Arthromeris cuneata Ching
  1971 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *2029* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Drymotaenium miyoshianum (Makino) Makino
  2058 (HIB).

Lepidogrammitis drymoglossoides (Baker) Ching (syn.: *Lemmaphyllum drymoglossoides* Baker)
  2027 (A, CM, HIB, NAS, PE, UC).

Lepidogrammitis elongata Ching*, Fl. Tsinlingensis **2:** 232. 1974.
  553 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1363* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Lepisorus asterolepis (Baker) Ching*, Jiangsu Zhi Wu Zhi (Fl. Jiangsuensis) **1:** 74. *fig. 112.* 1977.
  1163 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Lepisorus contortus (Christ) Ching
  134 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *358* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Lepisorus distans (Tagawa) Ching*, Acta Phytotax. Sinica **10:** 302. 1965.
  1297 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Lepisorus marginatus Ching, Fl. Tsinlingensis **2:** 233. 1974.
  15 (A, HIB, NAS, NY, PE, UC); *61* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *515* (A, CM, HIB, KUN, NA, NAS, PE, UC).

Lepisorus paohuashanensis Ching*, Jiangsu Zhi Wu Zhi (Fl. Jiangsuensis) **1:** 467. *fig. 113.* 1977.
  962 (A, HIB, PE, UC).

Lepisorus thunbergianus (Kaulf.) Ching
  1817 (A, HIB).

Microsorium fortunei (Moore) Ching
  426 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *556* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1430* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Microsorium subhastatum (Baker) Ching (distributed as *Lepidomicrosorium subhastatum* (Baker) Ching)
  2083 (A, CM, HIB, NY, PE, UC).

Neolepisorus ovatus (Bedd.) Ching, Acta Phytotax. Sinica **9:** 99. 1964, forma *deltoidea* (Baker) Ching, *ibid.*
  247 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1431* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Polypodioides pseudo-amoenum (Ching) Ching, comb. nov.
  BASIONYM: *Polypodium pseudo-amoenum* Ching, Fl. Tsinlingensis **2:** 177. 1974.

332 (A, CM, HIB, KUN, NAS, PE, UC); *356* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Pyrrosia assimilis (Baker) Ching*
805 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Pyrrosia caudifrons Ching, Boufford, & Shing, sp. nov. FIGURE 7, d–g.

Species configuratione proxime affinis Pyrrosia linguae (Thunb.) Farw., sed in fronde ambitu elliptica ad apicem caudata, stipitis longitudine aliquanto superante, textura tenuiore, differt, necnon P. heteractae (Mett.) Ching valde similis, sed statura minore, pilis stellatis solum e brachiis lanceolatis constitutis, differt.

Plants 20–22 cm tall. Rhizome wide-creeping, ca. 2 mm in diameter, densely covered with lanceolate, brown scales with ciliate margins. Fronds distant, 4–5 cm apart. Stipe 10–12 cm long, firm, dark-stramineous, glabrous above base; lamina 13–15 cm long, 3–4 cm wide at middle, elliptic, caudate at apex, cuneate at base, subcoriaceous, buff colored, glabrous above, covered beneath with thin tomentum of 1-layered, uniform, appressed stellate hairs consisting only of lanceolate arms, the lateral veins distinct to leaf margin, obliquely ascending. Sori subrounded or oblong, dense, in close rows of 4 or 5 between lateral veins, light colored when young, dark red at maturity.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), vicinity of Duanjiangping, 11 September 1980, *Sino-Amer. Bot. Exped. 1159* (holotype, PE; isotypes, A, CM, E, HIB, KUN, KYO, NA, NAS, NY, SFDH, UC, WH).

ADDITIONAL SPECIMENS EXAMINED. **China.** HUBEI: Hefeng, *H. J. Li 6840, 8393* (PE). SICHUAN: Emei Shan (Mt. Omei), *K. H. Shing & K. Y. Long 519, 525, 1163* (PE); Tieanjuan, *K. J. Kuan et al. 2330* (PE); Leipo, *Z. T. Kuan 8426* (PE); Daxiang Ling, *S. S. Kung 3691* (PE).

Pyrrosia caudifrons is similar to *P. lingua* (Thunb.) Farw. in habit, but differs in the elliptic outline, caudate apices, and thinness of the fronds, which are slightly longer than the stipe. *Pyrrosia caudifrons* is also very similar to *P. heteracta* (Mett.) Ching in habit, but differs mainly from this species in its smaller size and in the stellate hairs on the undersurface of the fronds consisting of only lanceolate arms. The stellate hairs in *P. heteracta* have both lanceolate and aciculate arms.

Pyrrosia drakeana (Franchet) Ching
18 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *519* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1816* (A, HIB).

Pyrrosia gralla (Giesenh.) Ching*
1714 (A, HIB, PE, UC).

Pyrrosia lingua (Thunb.) Farw.
1929 (A, CM, HIB, NA, NAS, PE, UC).

Pyrrosia mollis (Kunze) Ching
547 (A, HIB, UC).

Pyrrosia petiolosa (Christ) Ching
438 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Pyrrosia pseudocalvata Ching, Boufford, & Shing, sp. nov.

Species (critica ex affinitate) Pyrrosia calvatae (Baker) Ching valde simile (cui ambitu congruit), sed in pilis stellatis deciduis e branchiis aciculatis brunneis, aliter glabra, recedit.

Plants 40–67 cm tall. Rhizome short, thick, procumbent, ca. 6 mm in diameter, densely covered with lanceolate, brown scales with ciliate margins. Fronds proximate. Stipe 8–13 cm long, greenish stramineous, glabrous above base; lamina 30–50 cm long, 2.5–3 cm wide at middle, lanceolate, acuminate at apex, gradually narrowed at base, decurrent, coriaceous, both sides yellow-green, glabrous above, sparsely covered beneath with single layer of deciduous, stellate hairs with aciculate arms; veins indistinct. Sori subrounded, densely covering undersurface from middle to apex, yellow-green when young, brown at maturity.

TYPE. China, western Hubei Province, Xingshan Xian (31°05′N, 110°30′E), ca. 1 km W of the Leigutai Hydroelectric Power Station at the confluence of the Jiuchong and Dangyang rivers, elevation ca. 390 m; steep rocky slope, 5 September 1980, *Sino-Amer. Bot. Exped. 1110* (holotype, PE; isotypes, A, CM, HIB, KUN, NA, NAS, NY, UC).

ADDITIONAL SPECIMENS EXAMINED. **China.** GANSU: Wen Xian, *Y. Q. He 1337* (PE). GUIZHOU: Xingyi, *An-Shun Exped. 640* (PE); Qingzhen, *Sichuan-Guizhou Exped. 2166* (PE); Zunyi, *Sichuan-Guizhou Exped. 1405* (PE). HUBEI: Shennongjia Forest District (31°30′N, 110°30′E), Honghua ravine on W side of Dangyang R. N of Honghua, elev. ca. 820 m, growing on rock in forest, *1980 Sino-Amer. Bot. Exped. 1429* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); Shennongjia Forest District, vic. of Houshanping on S side of Hou R., elev. 800–1050 m, *1980 Sino-Amer. Bot. Exped. 1663* (A, CM, HIB, NA, NAS, NY, PE); Badong, *H. C. Chow 957* (PE); Enshi, *H. C. Chow 1940* (PE); He-feng, *H. J. Li 4949* (PE). HUNAN: Mang Shan, *K. Z. He 4938* (PE). SHANXI: Pingli, *K. Y. Bei 20* (PE). SICHUAN: Emei Shan (Mt. Omei), *K. H. Shing & K. Y. Long 1083* (PE); Zhenkou, *T. L. Dai 100121, 102488, 104590, 107167, 107796* (PE).

Because of the similarity in general outline of the fronds, *Pyrrosia pseudocalvata* has been considered identical to *P. calvata* (Baker) Ching. It differs in having only a single layer of sparse, deciduous, stellate hairs with aciculate arms instead of a double layer, of which the ground layer consists of stellate hairs with usually persistent, wooly arms. The geographic distribution of the species also differs: *P. calvata* occurs in Guangdong, Guangxi, Yunnan, Fujian, and southern Zhejiang provinces, and the two meet only in Guizhou Province.

Pyrrosia sheareri (Baker) Ching
1925 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *2055* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Saxiglossum angustissimum (Giesenh.) Ching, Acta Phytotax. Sinica **10:** 301. 1965.
428 (A, CM, HIB, KUN, NA, NAS, PE, UC); *697* (A, CM, HIB, KUN, NA, NAS, NY,

PE, SFDH, UC, WH); *852* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

LOXOGRAMMACEAE

Loxogramme grammitoides (Baker) C. Chr.*
546 (A, HIB).
Loxogramme saziran Tagawa*
427 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *514* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1294* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

AZOLLACEAE

Azolla imbricata (Roxb.) Nakai
2056 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

GYMNOSPERMAE

TAXACEAE

Amentotaxus argotaenia (Hance) Pilger
533 (A, HIB, NA).
Taxus chinensis (Pilger) Rehder
585 (A, HIB); *777* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1540* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1824* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Torreya fargesii Franchet
584 (A, HIB); *625* (HIB).

CEPHALOTAXACEAE

Cephalotaxus fortunei Hooker f.
751 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1038* (A, CM, E, HIB, KUN, NAS, NY, PE, SFDH, UC, WH).
Cephalotaxus sinensis (Rehder & Wilson) H. L. Li
104 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1759* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1829* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

PINACEAE

Abies fargesii Franchet
958 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Keteleeria davidiana (Bertr.) Beiss.
244 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Picea wilsonii Mast.
126 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1823* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Pinus armandii Franchet

384 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC); *877* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Pinus massoniana Lamb.
1729 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Pinus massoniana Lamb. var. *henryi* (Mast.) Wu, Acta Phytotax. Sinica **5:** 153. 1956.
1466 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Tsuga chinensis (Franchet) Pritzel
1385 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1827* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

CUPRESSACEAE

Cupressus funebris Endl.
1914 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

TAXODIACEAE

Metasequoia glyptostroboides Hu & Cheng
2082 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

ANGIOSPERMAE

Dicotyledones

SAURURACEAE

Houttuynia cordata Thunb.
468 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

CHLORANTHACEAE

Chloranthus multistachys Péi
456 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1699* (A, CM, HIB, KUN, NA, PE).

SALICACEAE

Populus davidiana Dode
1388 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Populus lasiocarpa Oliver*
1343 (A, HIB).

Populus wilsonii Schneider
742 (A, HIB).

Salix fargesii Burkill
1815 (A, HIB).

Salix fargesii Burkill var. *kansuensis* (Hao) N. Chao, Feddes Repert. Spec. Nov. Regni Veg. Beih. **93:** 61. 1936.
235 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

JUGLANDACEAE

Juglans cathayensis Dode
450 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, WH).
Platycarya strobilacea Sieb. & Zucc.
1574 (A, CM, HIB, KUN, NA, NAS, PE).
Pterocarya delavayi Franchet*
1544 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Pterocarya hupehensis Skan
940 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Pterocarya paliurus Batalin (syn.: *Cyclocarya paliurus* (Batalin) Iljinskaja)
1299 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Pterocarya stenoptera DC.
1573 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

BETULACEAE

Betula albo-sinensis Burkill
31 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Betula cf. *albo-sinensis* Burkill
897 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

This collection may represent a hybrid between *Betula albo-sinensis* and *B. utilis* D. Don, another species credited to the Shennongjia region (Anonymous, 1980) but not collected by the 1980 Sino-American Botanical Expedition.

Betula fargesii Franchet
904 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Betula insignis Franchet
183 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Betula luminifera H. Winkler
734 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Carpinus chinensis (Franchet) Cheng (syn.: *C. cordata* Blume var. *chinensis* Franchet, J. Bot. **13:** 202. 1899.)
1528 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Carpinus fargesii Franchet
1011 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Carpinus hupeana Hu
1548 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Carpinus simplicidentata H. H. Hu
1009 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1486* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Corylus ferox Wallich var. *tibetica* (Batalin) Franchet, J. Bot. **13:** 200. 1899.
12 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *346* (A, HIB, NA, PE); *383* (A, CM, HIB, PE); *1048* (A, HIB, NAS, NY, PE, UC).
Corylus heterophylla Fischer ex Trautv. var. *sutchuenensis* Franchet, J. Bot. **13:** 199. 1899.
214 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *613* (A, CM,

HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1255* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1882* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Corylus mandshurica Maxim. & Rupr.* (syn.: *C. sieboldiana* Blume var. *mandshurica* (Maxim. & Rupr.) Schneider, Pl. Wilsonianae **2:** 454. 1916.)
1535 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

An interesting species with a discontinuous distribution from Sichuan (and now western Hubei) in central China, to northeastern China and Korea, and the northern Japanese island of Hokkaido. (See Schneider, Pl. Wilsonianae **2:** 454. 1916, for additional details of distribution.)

Corylus yunnanensis (Franchet) A. Camus
1230 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

FAGACEAE

Castanea henryi (Skan) Rehder & Wilson
1852 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Castanea mollissima Blume
463 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *798* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1427* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1884* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *2034* (A, HIB).

Fagus engleriana Seem.
1221 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1309* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Fagus longipetiolata Seem.
1479 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Fagus lucida Rehder & Wilson
1485 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Lithocarpus cleistocarpus (Seem.) Rehder & Wilson
728 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lithocarpus polystachyus (Wallich ex DC.) Rehder*
1126 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Quercus acutidentata (Maxim.) Koidz.
378 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *743* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1858* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Quercus engleriana Seem.
577 (A, HIB, UC).

Quercus glandulifera Blume
1193 (A, HIB, PE); *1883* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1931* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Quercus glandulifera Blume var. *brevipetiolata* (A. DC.) Nakai, J. Arnold Arbor. **5:** 76. 1924.
778 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Quercus glauca Thunb. var. *gracilis* (Rehder & Wilson) A. Camus, Les Chênes **1:** 285. 1938.
67 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

In Fl. Hupehensis **1:** 116. 1976, this taxon is elevated to the rank of species, and a new combination—*Quercus gracilis* (Rehder & Wilson) Wuzhi—is made. This name is invalid as a later homonym of *Quercus gracilis* Korth. Verh. Nat. Gesch. Bot. 207. 1844.

Quercus myrsinifolia Blume
729 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Quercus oxyodon Miq.
576 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC); *1065* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Quercus spinosa David ex Franchet
371 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1310* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

ULMACEAE

Celtis biondii Pampan.
432 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *789* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Celtis vandervoetiana Schneider*
1490 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Zelkova sinica Schneider
1706 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

MORACEAE

Broussonetia papyrifera (L.) L'Hér. ex Vent.
414 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1585* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Ficus foveolata Wallich var. *henryi* King ex Oliver, Hooker's Icon. Pl. **19:** *pl. 1824*. 1889. (syn.: *F. sarmentosa* Buch.-Ham. ex J. E. Smith var. *henryi* (King) Corner (Gard. Bull. Singapore **18:** 6. 1960.) in Fl. Hupehensis **1:** 152. 1976.)
1603 (A, CM, HIB, PE, UC).

Ficus heteromorpha Hemsley
550 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1074* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1451* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Ficus impressa Champ. (syn.: *F. sarmentosa* Buch.-Ham. ex J. E. Smith var. *impressa* (Champ.) Corner, Gard. Bull. Singapore **18:** 6. 1960.)
1492 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

CANNABINACEAE

Cannabis sativa L.
651a (pistillate) (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *651b* (staminate) (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Humulus scandens (Lour.) Merr. (syn.: *H. japonicus* Sieb. & Zucc.)
1639 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

URTICACEAE

Boehmeria diffusa Wedd.
482 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Boehmeria gracilis C. H. Wright
793 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Elatostema ichangense H. Schroter*
1919 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Elatostema stewardii Merr.
824 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Gonostegia hirta (Blume) Miq.
1937 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Lecanthus peduncularis (Royle) Wedd.*
494 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Oreocnide frutescens (Thunb.) Miq. (syn.: *O. fruticosa* (Gaudich.) Hand.-Mazz.)
1638 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Parietaria micrantha Ledeb. (syn.: *P. debilis* Forster var. *micrantha* (Ledeb.) Wedd. in DC. Prodr. **16**(1): 235^{45}. 1869.)
1833 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Pilea japonica (Maxim.) Hand.-Mazz.
534 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Pilea martinii (Lévl.) Hand.-Mazz.
488 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Pilea plataniflora C. H. Wright
1113 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1660* (A, HIB, KUN, NA, NAS, NY, PE, UC).

Pilea sinofasciata C. J. Chen & B. Bartholomew, nom. nov., based on *Pilea fasciata* Franchet, Nouv. Arch. Mus. Hist. Nat. II. **10:** 81. 1888, non Wedd. in DC. Prodr. **16**(1): 120. 1869.
1362 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

LORANTHACEAE

Loranthus levinei Merr.
1324 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

ARISTOLOCHIACEAE

Aristolochia heterophylla Hemsley
1121 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Saruma henryi Oliver
1592 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

BALANOPHORACEAE

Balanophora involucrata Hooker f.
889 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1260* (HIB).

Balanophora japonica Makino
458 (HIB); *890* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

POLYGONACEAE

Antenoron neofiliforme (Nakai) Hara
422 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *764* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Polygonum amplexicaule D. Don var. *sinense* Forbes & Hemsley, J. Linn. Soc., Bot. **26:** 333. 1891.
202 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *501* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Polygonum caespitosum Blume
1347 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1956* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1957* (A, HIB, NA, PE).

Polygonum ciliinerve (Nakai) Ohwi (syn.: *P. multiflorum* Thunb. var. *ciliinerve* (Nakai) A. N. Steward, Contr. Gray Herb. **88:** 97. 1930.)
307 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Polygonum cuspidatum Sieb. & Zucc.
437 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *724* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1578* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1626* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Polygonum hydropiper L.
1954 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Polygonum multiflorum Thunb.
440 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1657* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Polygonum muricatum Meisner (syn.: *P. strigosum* R. Br. var. *muricatum* (Meisner) A. N. Steward, Contr. Gray Herb. **88:** 89. 1930.)
1955 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *2013* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Polygonum persicaria L.*
1521 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *2015* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Polygonum pilosum (Maxim.) Forbes & Hemsley
41 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Polygonum thunbergii Sieb. & Zucc.
1953 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

AMARANTHACEAE

Achyranthes aspera L.
562 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1501* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Achyranthes bidentata Blume
491 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Celosia argentea L.
1918 (A, HIB, NA, NAS, NY, PE).

PHYTOLACCACEAE

Phytolacca acinosa Roxb.
1826 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Phytolacca cf. *polyandra* Batalin*
723 (A, HIB, KUN, NAS, NY, PE, SFDH, UC, WH).

Nowicke (Ann. Missouri Bot. Gard. **55:** 294–364. 1968) did not see specimens of *Phytolacca polyandra* Batalin and therefore did not treat this species in her study of the Phytolaccaceae. Although our specimens have five (not eight) united carpels and sterile (not fertile) stamens, they agree most closely with the original description of that species. Nowicke admitted that her treatment of *Phytolacca* was not exhaustive and stated that the genus is in need of further, critical study.

CARYOPHYLLACEAE

Cucubalus baccifera L.
409 (A, HIB, PE, UC).
Dianthus superbus L.
144 (HIB); *945* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Silene fortunei Vis.
780 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1409* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1917* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Silene linearifolia Pampan.
973 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Silene tatarinowii Regel (syn.: *Melandrium tatarinowii* (Regel) Y. W. Tsui)
71 (A, HIB, KUN, NA, NAS, NY, PE, UC); *386* (A, CM, HIB, KUN, NA, NAS, PE, UC); *1859* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

TETRACENTRACEAE

Tetracentron sinense Oliver
1183 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

EUPTELEACEAE

Euptelea pleiosperma Hooker & Thomson
105 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *216* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1151* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1549* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

RANUNCULACEAE

Aconitum cannabifolium Franchet
1290 (A, CM, HIB, KUN, NA, NAS, NY, PE).

Aconitum hemsleyanum Pritzel

69 (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *154* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *388* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1156* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1320* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1777* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Aconitum scaposum Franchet

136 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *191* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *357* (A, HIB); *421* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH).

Actaea asiatica Hara

413 (HIB); *1387* (A, HIB); *1835* (A, HIB, NA, PE).

Anemone hupehensis Lemoine

754 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Anemone tomentosa (Maxim.) Péi

53 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Aquilegia oxysepala Trautv. & Meyer*

258 (A, HIB, KUN, NA, NAS, NY, PE, UC); *869* (A, HIB, KUN, NA, PE, UC).

Cimicifuga acerina (Sieb. & Zucc.) Tanaka

586 (A, CM, HIB, NA, NAS, PE); *622* (A, HIB); *1361* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cimicifuga foetida L.*

253 (A, HIB, NY, UC).

Cimicifuga simplex Wormsk.

57 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Clematis gratopsis W. T. Wang

1439 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1905* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Clematis lasiandra Maxim.

1 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *181* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *217* (A, CM, E, HIB, KUN, MO, NA, NAS, NY, PE, SFDH, UC, WH); *310* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *700* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1192* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1328* (A, HIB, KUN, NA, NAS, NY, PE); *1648* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Clematis otophora Franchet

301 (A, CM, HIB, KUN, NAS, NY, PE, UC); *635* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1546* (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Clematis uncinata Champ. var. *coriacea* Pampan. Nuovo Giorn. Bot. Ital. **22:** 288. 1915.

580 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Clematis urophylla Franchet*

1940 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Delphinium potaninii Huth*

405 (A, HIB, PE).

Paeonia obovata Maxim. var. *willmottiae* (Stapf) Stern, J. Roy. Hort. Soc. **68:** 128. 1943.

197 (A, HIB); *385* (A, HIB, KUN, NAS, PE, UC).

Thalictrum przewalskii Maxim.
159 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Thalictrum robustum Maxim.
572 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Thalictrum uncinulatum Franchet
148 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

LARDIZABALACEAE

Akebia trifoliata (Thunb.) Koidz.
677 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1089* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Decaisnea fargesii Franchet
72 (A, CM, HIB, NY, PE); *618* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1055* (A, HIB, PE, UC).
Holboellia fargesii Réaubourg
616 (A, HIB); *1005* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1704* (A, CM, HIB, NA, NAS, PE).
Sinofranchetia chinensis (Franchet) Hemsley
1241 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1879* (A, HIB, NY, PE, SFDH, UC).

BERBERIDACEAE

Berberis circumserrata (Schneider) Schneider
255 (A, CM, HIB, KUN, NA, NY, PE, UC).
Berberis dasystachya Maxim.
204 (A, HIB, KUN, NY, PE, UC); *341* (HIB); *888* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Berberis feddeana Schneider*
1782 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Berberis henryana Schneider
373 (A, HIB, PE, UC); *1232* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Berberis julianae Schneider
232 (A, CM, HIB, KUN, NAS, NY, PE, UC); *1804* (A, CM, HIB, KUN, NA, NY, PE).
Berberis mitifolia Stapf*
1204 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1553* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH);*1861* (A, HIB, KUN, NA, NAS, PE, SFDH, WH).
Berberis sargentiana Schneider
472 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1938* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Berberis triacanthophora Fedde
643 (A, CM, HIB, KUN, NA, NAS, PE, UC).
Berberis virgetorum Schneider
2079 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Caulophyllum robustum Maxim.
911 (HIB); *1202* (A, HIB, KUN, MO, NA, NAS, NY, PE, UC).

Diphylleia sinensis H. L. Li
910 (A, HIB).
Epimedium davidii Franchet
1869 (A, HIB).
Nandina domestica Thunb.
1101 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

MENISPERMACEAE

Sinomenium acutum (Thunb.) Rehder & Wilson
696 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1067* (A, CM, HIB, KUN, NA, NAS, NY, PE).
Stephania sinica Diels
698 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Tinospora sagittata (Oliver) Gagnep.
1716 (A, HIB, PE).

MAGNOLIACEAE

Magnolia sprengeri Pampan.*
1181 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

ILLICIACEAE

Illicium henryi Diels
512 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1028* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1491* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

SCHISANDRACEAE

Schisandra glaucescens Diels
86 (HIB); *101* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *199* (HIB); *331* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *382* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH); *645* (A, CM, HIB, KUN, NA, PE, UC); *711* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC); *1389* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

LAURACEAE

Actinodaphne cf. *reticulata* Meisner var. *forrestii* Allen, Ann. Missouri Bot. Gard. **25:** 412. 1937.
1070 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Lindera communis Hemsley
1423 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1650* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1679* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1906* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Lindera fragrans Oliver
1623 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Lindera fruticosa (Hemsley) Gamble

765 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1481* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lindera glauca (Sieb. & Zucc.) Blume

447 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *782* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC).

Lindera megaphylla Hemsley

1900 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lindera obtusiloba Blume

1308 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lindera subcaudata (Merr.) Merr.*

704 (A, HIB).

Litsea ichangensis Gamble

303 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *510* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *631* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1812* (A, CM, HIB, PE).

Litsea aff. *sericea* (Nees) Hooker f.*

316 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *892* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1587* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1877* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Neolitsea confertifolia (Hemsley) Merr.

412 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *583* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *603* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1027* (A, CM, HIB, KUN, NAS, NY, PE); *1085* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1495* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1608* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Phoebe neurantha (Hemsley) Gamble

2045 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

PAPAVERACEAE

Macleaya microcarpa (Maxim.) Fedde

300 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Stylophorum lasiocarpum (Oliver) Fedde

84 (A, HIB); *1064* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

FUMARIACEAE

Corydalis davidii Franchet

399 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *859* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Corydalis incisa (Thunb.) Pers.

176 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

CRUCIFERAE

Arabis pendula L.

1153 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cardamine urbaniana O. E. Schulz

1800 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rorippa indica (L.) Hieron.
1020 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

CRASSULACEAE

Sedum aizoon L.
107 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1212* (A, HIB).
Sedum amplibracteatum K. T. Fu, Fl. Tsinlingensis **1**(2): 425. 1974. (a nomen novum for *S. bracteatum* Diels, non *S. bracteatum* Viv.)
203 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1001* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Sedum dielsii Hamet
1634 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Sedum erythrostictum Miq.* (syn.: *S. telephium* L. subsp. *alboroseum* (Baker) Fröd. Acta Horti Gothob. **5**(Appendix): 61. 1930.)
1210 (A, HIB).
Sedum filipes Hemsley
589 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *776* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *974* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Sedum verticillatum L.
173 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

SAXIFRAGACEAE

Astilbe rubra Hooker & Thomson
75 (A, CM, HIB, NAS, PE, UC).
Chrysosplenium lanuginosum Hooker & Thomson* (incl. *C. ciliatum* Franchet)
1206 (A, HIB).
Chrysosplenium macrophyllum Oliver
1208 (A, HIB).
Chrysosplenium pilosum Maxim. var. *valdepilosum* Ohwi, Repert. Spec. Nov. Regni Veg. **36**: 52. 1934.
1207 (A, HIB).
Decumaria sinensis Oliver
1454 (A, HIB, NA, NAS, NY, PE, UC); *1899* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Deutzia schneideriana Rehder*
1615 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Deutzia vilmorinae Lemoine
16 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *149* (A, CM, HIB, NAS, NY, PE); *349* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *539* (A, CM, HIB, NA, NAS, PE); *1032* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Dichroa febrifuga Lour.
1972 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Hydrangea aspera D. Don subsp. *robusta* (Hooker & Thomson) McClint. Proc. Calif. Acad. Sci. **29**: 194. 1957.

370 (A, HIB, KUN, NA, NAS, NY, PE, UC); *606* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1197* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1353* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Hydrangea aspera D. Don subsp. *strigosa* (Rehder) McClint. Proc. Calif. Acad. Sci. **29:** 193. 1957.

467 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *693* (A, HIB, KUN, NA, NAS, NY, PE, UC); *1106* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1913* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Hydrangea heteromalla D. Don

128 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *184* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *370a* (A); *735* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *884* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *899* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1341* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1529* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1772* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Hydrangea scandens (L. f.) Sér. subsp. *chinensis* (Maxim.) McClint. Proc. Calif. Acad. Sci. **29:** 206. 1957.

2003 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Itea ilicifolia Oliver

1107 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Parnassia delavayi Franchet

37 (A, CM, HIB, KUN, NA, PE, UC).

Parnassia wightiana Wallich ex Arnott

1186 (A, HIB, PE, UC).

Philadelphus incanus Koehne

230 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *518* (A, HIB, NA, NAS, NY, PE); *748* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1026* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1614* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Philadelphus sericanthus Koehne

188 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *956* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC).

Ribes acuminatum Wallich

40 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *112* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *158* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH); *252* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Ribes fasciculatum Sieb. & Zucc. var. *chinense* Maxim. Mélanges Biol. Bull. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg **9:** 237. 1873; Bull. Acad. Imp. Sci. Saint-Pétersbourg **19:** 264. 1874.

1682 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Ribes moupinense Franchet

647 (A, HIB, PE); *969* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Ribes sp.

167 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rodgersia aesculifolia Batalin

79 (A, HIB); *900* (A, CM, HIB, KUN, NA, PE).

Saxifraga flabellifolia Franchet
308 (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Saxifraga giraldiana Engler var. *hupehensis* Engler, Bot. Jahrb. Syst. **29:** 366. 1901.
26 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *172* (A, CM, HIB, NA, NAS, NY, PE, UC).

Schizophragma integrifolium Oliver
582 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1291* (A, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Tiarella polyphylla D. Don
1864 (A, HIB, KUN, PE, UC).

PITTOSPORACEAE

Pittosporum glabratum Lindley var. *neriifolium* Rehder & Wilson, Pl. Wilsonianae **3:** 328. 1916.
2030 (A, HIB).

Pittosporum rehderianum Gowda
478 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1066* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1438* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1640* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Pittosporum truncatum Pritzel
1616 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

HAMAMELIDACEAE

Corylopsis platypelta Rehder & Wilson
1300 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Corylopsis sinensis Hemsley
752 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Corylopsis veitchiana Bean
2033 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Liquidambar acalycina Chang, Bull. Sun Yat-sen Univ. **2:** 33. 1959; Fl. Reip. Pop. Sinicae **35**(2): 56. 1979.
1950 (A, HIB, NAS, NY, PE, UC).

Sinowilsonia henryi Hemsley
1483 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Sycopsis sinensis Oliver
248 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

ROSACEAE

Agrimonia pilosa Ledeb.
451 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Cotoneaster acutifolius Turcz.
96 (A, CM, HIB, NAS, NY, PE, UC); *344* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *365* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC,

WH); *857* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1551* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1731* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster acutifolius Turcz. var. *villosulus* Rehder & Wilson, Pl. Wilsonianae **1:** 158. 1912.

13 (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH).

Cotoneaster bullatus Bios.

215 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC).

Cotoneaster dielsianus Pritzel

1016 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1044* (A, CM, HIB, KUN, NA, NAS, PE, UC); *1283* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1346* (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Cotoneaster aff. *dielsianus* Pritzel

1935 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster divaricatus Rehder*

1318 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster foveolatus Rehder & Wilson*

265 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *906* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC); *941* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1332* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1344* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1750* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster aff. *foveolatus* Rehder & Wilson

1854 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster horizontalis Dcne.

100 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *375* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *779* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1609* (A, HIB, KUN, NA, NAS, NY, PE, UC); *1830* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1933* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster multiflorus Bunge

1751 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1806* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1834* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster obscurus Rehder & Wilson*

129 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *205* (A, CM, HIB, NA, PE, UC); *211* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *393* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Cotoneaster salicifolius Franchet

676 (A, CM, HIB, KUN, NAS, PE, SFDH, UC, WH); *1086* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1907* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster salicifolius Franchet var. *rugosus* (Pritzel) Rehder & Wilson, Pl. Wilsonianae **1:** 172. 1912. (syn.: *C. rugosus* Pritzel)

520 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1708* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster aff. *zabellii* Schneider

575 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC); *1579* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cotoneaster sp.

372 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1801* (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Crataegus cuneata Sieb. & Zucc.*

1736 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Crataegus wilsonii Sarg.

9 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *70* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *263* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *896* (A, CM, HIB, NAS, NY, PE); *1056* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1234* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Fragaria gracilis A. Los.

164 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Kerria japonica (L.) DC.

221 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *350* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *579* (A, CM, HIB, NA, NAS, NY, PE); *1279* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Malus kansuensis (Batalin) Schneider*

36 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *262* (A, HIB, PE, UC); *397* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *893* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Malus yunnanensis (Franchet) Schneider*

571 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1556* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1771* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Malus yunnanensis (Franchet) Schneider var. *veitchii* Hort. ex Rehder, J. Arnold Arbor. **4**: 115. 1923.

1301 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Malus sp.

106 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *484* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *767* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1218* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, UC); *1298* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1314* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1745* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1807* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1885* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

The collections of *Malus* listed above have been quite difficult to identify, although all (with the possible exception of *1298*) are referable to either *M. hupehensis* or *M. halliana* Koehne. It has become apparent, however, that the relationships of these two species are in need of careful assessment and resolution before the above-listed collections can be named with any assurance. Unfortunately, time has not allowed more than a casual investigation of this problem, but it is hoped that further collaborative work can soon be undertaken in both China and the United States.

Neillia sinensis Oliver
135 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *470* (A, HIB); *678* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1077* (A, HIB, NY, PE).

Photinia beauverdiana Schneider
770 (A, CM, HIB, KUN, NAS, PE, UC); *1543* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1583* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH); *1875* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Photinia beauverdiana Schneider var. *notabilis* (Schneider) Rehder & Wilson, Pl. Wilsonianae **1**: 188. 1912.
1022 (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH).

Photinia parvifolia (Pritzel) Schneider
2044 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *2081* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Photinia villosa (Thunb.) DC.
1865 (A, HIB, NA, PE, SFDH, UC).

Potentilla fruticosa L.
120 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1184* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Potentilla leuconota D. Don
937 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Prunus brachypoda Batalin
967 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Prunus salicina Lindley
139 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *336* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Pyracantha crenulata (D. Don) Roemer
1903 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1961* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Pyracantha fortuneana (Maxim.) H. L. Li
436 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *466* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1417* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1622* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1939* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Pyrus pyrifolia (Burman f.) Nakai
847 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Pyrus serrulata Rehder*
1630 (A, CM, E, HIB, KUN, NAS, NY, PE, SFDH, UC, WH).

Rosa banksiae Aiton*
442 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1410* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1632* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rosa banksiopsis Baker
1778 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rosa helenae Rehder & Wilson
747 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Rosa henryi Boulenger
783 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Rosa omeiensis Rolfe
27 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *125* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rosa saturata Baker
268 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *960* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rosa sertata Rolfe
961 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Rosa sp.
10 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *147* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *187* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *732* (A, HIB); *876* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *957* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1053* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1406* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1534* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1633* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1784* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1862* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1863* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1934* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

A situation similar to that mentioned under the unidentified collections of *Malus* exists with the undetermined collections of *Rosa*. Although for the most part the collections fall into two or three groups, unclear or unresolved species limits and the possibility of hybridization have prevented assured determinations and indicate the need for further work.

Rubus amphidasys Focke ex Diels
2076 (A, CM, HIB, NAS, NY, PE).

Rubus flosculosus Focke
5 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1545* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rubus ichangensis Hemsley & Kuntze*
551 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rubus innominatus S. Moore
449 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Rubus lambertianus Sér.*
499 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *502* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *799* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1422* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1637* (A, CM, HIB, KUN, NA, NAS, NY, PE, UC); *1936* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rubus lasiostylus Focke
229 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1058* (A, HIB, KUN, NA, NAS, NY, PE); *1312* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rubus lasiostylis Focke var. **hubeiensis** Yü, Spongberg, & Lu, var. nov.

A varietate lasiostylo in drupeolis indumento minore praeditis, aurantiaco-rubrae, et stylo parte distili glabro deciduo, differt.

Differing from var. *lasiostylus* in having less densely pubescent, orange-red drupelets and distally glabrous, deciduous styles.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E), on a steep, NW-facing slope above the road to Chuifeng Pass, elevation ca. 2780 m; shrub 1.5–2 m tall, fruits red, 1–1.5 cm across, the young stems grayish, bark on older stems brownish red, 26 August 1980, *Sino-Amer. Bot. Exped. 114* (holotype, PE; isotypes, A, HIB, KUN, NA, NAS, NY, SFDH, UC, WH).

ADDITIONAL SPECIMENS EXAMINED. **China.** HUBEI: Shennongjia Forest District (31°30′N, 110°30′E), NW-facing slope below Chuifeng Pass in *Sinarundinaria* thickets and in disturbed meadow with *Abies chensiensis,* elev. ca. 2900 m; shrubs with orange-red, sweet, edible fruits, *1980 Sino-Amer. Bot. Exped. 155* (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rubus lasiostylus var. *hubeiensis* can be distinguished from var. *lasiostylus* by its less densely pubescent drupelets, by its distally glabrous (vs. pubescent) styles that tend to be deciduous (vs. persistent) prior to drupelet maturity, and by the orange-red color (pinkish when dry) of the drupelets (vs. whitish; tannish when dry). Based on the limited material available for comparison, other characters that may be of significance include the relative lack of prickles on the floricanes and an apparent difference in stipule and infructescence-bract shape. In var. *lasiostylus* the floricanes are usually beset with numerous straight to slightly recurved, spreading prickles, and the stipules and bracts of the infructescence are narrowly lanceolate. By contrast, the stipules and bracts of var. *hubeiensis* tend to be ovate to suborbiculate.

As in *Rubus lasiostylus* var. *dizygos* Focke (*in* Pl. Wilsonianae **1:** 53. 1911), the leaves on the flowering shoots of var. *hubeiensis* sometimes bear five (rather than three) leaflets. In other details of the vegetative parts, fruit aggregates, and seeds, var. *hubeiensis* agrees with var. *lasiostylus.*

Rubus setchuenensis Bur. & Franchet
1952 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rubus simplex Focke
1130 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Sorbaria arborea Schneider
7 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *266* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *971* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1025* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Sorbus alnifolia (Sieb. & Zucc.) K. Koch
377 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1302* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1400* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1779* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1855* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Sorbus caloneura (Stapf) Rehder
753 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1097* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *2039* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Sorbus folgneri (Schneider) Rehder
1008 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1476* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1870* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Sorbus hupehensis Schneider
102 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *879* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1315* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Sorbus keissleri Rehder
1285 (A, HIB, KUN, NA, NAS, NY, PE, UC).

Sorbus koehneana Schneider
880 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *964* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Sorbus xanthoneura Rehder
719 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1317* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1342* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1739* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1776* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Sorbus zahlbruckneri Schneider
1555 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1728* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Spiraea chinensis Maxim.*
1610 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Spiraea japonica L. f. var. *acuminata* Franchet, Nouv. Arch. Mus. Hist. Nat. II. **8**: 218. 1886; Pl. David. **2**: 36. 1888.
8 (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC, WH); *444* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *781* (A, CM, HIB, NY, PE); *882* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Spiraea veitchii Hemsley
269 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *389* (A, CM, HIB, KUN, NA, NAS, NY, PE, UC); *860* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1155* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Stranvaesia amphidoxa Schneider (syn.: *Photinia amphidoxa* (Schneider) Rehder & Wilson)
2001 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Stranvaesia davidiana Dcne.*
209 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *213* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *513* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *614* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *772* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1039* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1081* (A, CM, E, HIB, KUN,

NA, NAS, NY, PE, SFDH, UC, WH); *1496* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Stranvaesia davidiana Dcne. var. *undulata* (Dcne.) Rehder & Wilson, Pl. Wilsonianae **1**: 192. 1912.
2035 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

LEGUMINOSAE

Amphicarpaea trisperma Baker
707 (A, HIB); *786* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1661* (A, HIB, NA, PE).
Bauhinia hupehana Craib
1109 (HIB).
Caesalpinia sepiaria Roxb.
1114 (A, HIB).
Campylotropis ichangensis Schindler
565 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cercis chinensis Bunge
1010 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1695* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cercis racemosa Oliver*
1115 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Dalbergia dyeriana Prain & Harms
1428 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1624* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Dalbergia mimosoides Franchet
803 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1421* (A, CM, HIB, PE); *1572* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Desmodium oldhamii Oliver
1526 (A, HIB, KUN, NA, NAS, PE, UC).
Desmodium podocarpum DC. subsp. *podocarpum*
1525 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Desmodium podocarpum DC. subsp. *fallax* (Schindler) Ohashi in Hara, Fl. E. Himalaya **2**: 65. 1971. (see also Ohashi, 1973)
1068 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Desmodium podocarpum DC. subsp. *oxyphyllum* (DC.) Ohashi in Hara, Fl. E. Himalaya **2**: 65. 1971, var. *oxyphyllum**
804 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1499* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Indigofera amblyantha Craib
337 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1732* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Indigofera pseudotinctoria Matsum.
1407 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Lespedeza buergeri Miq.
1607 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1860* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lespedeza cuneata (Dum.-Cours.) G. Don
703 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Lespedeza thunbergii (DC.) Nakai*
4 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *56* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1744* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Vicia cracca L.
1134 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Vicia pseudo-orobus Fischer & Meyer
1856 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

GERANIACEAE

Geranium henryi Kunth
11 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, WH); *65* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Geranium sibiricum L.
1441 (A, CM, HIB, KUN, NA, NAS, PE, UC).

RUTACEAE

Euodia rutacarpa (Juss.) Bentham var. *bodinieri* (Dode) Huang, Acta Phytotax. Sinica **6:** 113. 1957.
1947 (A, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Euodia rutacarpa (Juss.) Bentham var. *officinalis* (Dode) Huang*, Acta Phytotax. Sinica **6:** 114. 1957.
1450 (A, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

In Hartley's recent revision (Gard. Bull. Sing. **34:** 91–131. 1981) both of the above-mentioned taxa of *Euodia* are included in *Tetradium ruticarpum* (A. Juss.) Hartley. Hartley's revision should be consulted for the basis of the division of the genera *Tetradium* Lour. and *Euodia* J. R. & G. Forster, as well as *Melicope* J. R. & G. Forster.

Zanthoxylum armatum DC. (syn.: *Z. planispinum* Sieb. & Zucc.)
433 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *797* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1029* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1408* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Zanthoxylum dissitum Hemsley
1602 (A, CM, HIB, KUN, NAS, NY, PE, UC); *1675* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Zanthoxylum undulatifolium Hemsley
633 (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

POLYGALACEAE

Polygala arillata Buch.-Ham.
189 (A, HIB, NY, PE).

Polygala tatarinowii Regel
684 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC); *1688* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Polygala wattersii Hance
1698 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

EUPHORBIACEAE

Acalypha australis L.
1973 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Bischofia polycarpa (Lévl.) Airy-Shaw
1103 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Euphorbia chrysocoma Lévl. & Vaniot
1200 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Euphorbia hylonoma Hand.-Mazz.
364 (A, HIB, KUN, NA, NAS, NY, PE); *1158* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Leptopus chinensis (Bunge) Pojark. (syn.: *Andrachne chinensis* Bunge)
1613 (A, HIB, NA, PE); *1678* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Mallotus contubernalis Hance
448 (A, CM, HIB, KUN, NAS, NY, PE, UC); *1644* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

DAPHNIPHYLLACEAE

Daphniphyllum longistylum Chien
1468 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Daphniphyllum macropodum Miq.*
605 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

BUXACEAE

Buxus microphylla Sieb. & Zucc. var. *sinica* Rehder & Wilson, Pl. Wilsonianae **2**: 165. 1914.
223 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1397* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Pachysandra terminalis Sieb. & Zucc.
309 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *648* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1203* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1330* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Sarcococca humilis Stapf (syn.: *S. hookeriana* Baillon var. *humilis* Rehder & Wilson, Pl. Wilsonianae **2**: 164. 1914.)
305 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, UC); *403* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *682* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1245* (A, HIB); *1350* (A, HIB, NY, PE); *1352* (A, CM, HIB, KUN, NA, PE); *1967* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Sarcococca ruscifolia Stapf
1912 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

ANACARDIACEAE

Rhus chinensis Miller
1445 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhus verniciflua Stokes
103 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

AQUIFOLIACEAE

Ilex fargesii Franchet
717 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1304* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1395* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1753* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1775* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Ilex macrocarpa Oliver
1909 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Ilex macropoda Miq.
1227 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Ilex pedunculosa Miq.
741 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Ilex pernyi Franchet
239 (A, HIB); *673* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *800* (A, CM, HIB, KUN, NA, NAS, NY, PE); *1094* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1131* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1625* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Ilex shennongjiaensis T. R. Dudley & S. C. Sun, sp. nov.

A Ilex sugerokii Maxim. ex Japonia et Taiwania persimilis et manifeste affinis sed ramulis primo non nisi puberulis; gemmis terminalis brevis stipitatis; foliis laminis aliquantum maioribus et crassioribus; petiolis et stipulis brevioribus; fructibus persaepe maioribus; calycibus maioribus glabris, sinubus non profundus, lobis maioribus eciliatis; stigmatibus maioribus sessilibus, lobis parus elevatis clare disjunctis aeque superpositis; pyrenis maioribus fere teretibus transversaliter circularis, dorsaliter bisulcatis et striatis, praecipue differt.

Single-trunked tree to 10 m tall, 25 cm d.b.h. Mature bark glossy, whitish gray. First-year branchlets rigid, reddish brown, glistening, very sparsely puberulent becoming glabrous, 1–1.5 mm in diameter; third- and fourth-year growth terete, glabrous, grayish brown, glossy, 3–4 mm in diameter; leaves borne predominantly on first- and second-year branchlets, rarely persisting on older growth. Terminal buds shortly stipitate, ovoid or ellipsoid, 3–4 mm long, acute; stipes 0.5–1 mm long, sparingly puberulent; bud scales glabrous or remotely puberulent, not ciliate along margins; internodes 2–6 mm long; stipules deciduous, subulate, 0.3–0.5 mm long, glabrous. Leaves with petiole 2.5–3(–4) mm long, deeply grooved on adaxial surface, only sparsely puberulent; blade elliptic-ovate, 2.5–4(–5) by (1–)1.5–2.5(–3) cm, acute to subobtuse and shortly mucronulate at apex, mucro 0.2–0.5 mm long and amber colored, short-attenuate or truncate to occasionally briefly cuneate at base and sparingly puberulent near petiole, thickly coriaceous, dark green, glossy and glabrous on upper surface, dull yellow-green on lower surface, the lateral veins obscure, 6 or 7 pairs, the midvein minutely puberulent, flattened to complanate or somewhat impressed on upper surface, conspicuously elevated and glabrous on lower surface, the margin serrulate-crenulate along ¾–½ of distal portion, with 3 to 7 serrulations per cm. Flowers unknown. Infructescences solitary and axillary; fruiting peduncles erect, 1–1.5 mm long, rigid, glabrous, with 2 ovate, obtuse-cuspidate, glabrous prophylls at or above middle; pedicels 5.5–12 mm long, stout, rigid, more or less dilated toward base of fruit. Fruits spheroid and often oblate, 8–12 mm broad, dark cherry-red, glossy, glabrous, sweet tasting; calyces generally persistent, explanate, 4–5 mm across, glabrous, with shallow sinuses and 4 to 6 obtuse to subacute lobes, the lobes 1–1.5 by 0.5–1 mm, glabrous, with apices and margins entire; stigmas sessile, flattened, 1.5–2 mm in diameter, circular, with 4 (or 5) narrowly elliptic-fusiform, scarcely raised, separate lobes 1 by 0.2–0.3 mm. Pyrenes 4 or 5 per fruit, oblong, nearly circular in cross section, 4–5 by 2.5–3 mm; dorsal surface moderately bisulcate, with 2 thin, prominent, raised marginal ribs and 1 raised medial rib; ventral and lateral surfaces smooth; endocarps cartilaginous.

TYPE. China, western Hubei Province, Shennongjia Forest District (31°30′N, 110°30′E); infrequent between Yinpo and Qiaodonggou canyon, on bank along road between Jiuhuping Forest Farm and Bancang, elevation ca. 2100 m, 19 September 1980, *Sino-Amer. Bot. Exped. 1554* (holotype, PE; isotypes, A, CM, E, HIB, KUN, KYO, NA, NAS, NY, SFDH, UC, WH).

ADDITIONAL SPECIMENS EXAMINED. **China.** HUBEI: Shennongjia Forest District (31°30′N, 110°30′E); infrequent at Miaogou canyon, ca. 4 km N of Jiuhuping, elev. ca. 1768 m, in thicket along edge of stream, *1980 Sino-Amer. Bot. Exped. 236* (A, HIB, NA, PE).

Ilex shennongjiaensis falls in ser. Cassinoides (Loes.) Hu of sect. PALTORIA (Ruiz & Pavon) Maxim. of subg. ILEX. The other Asiatic components of ser. Cassinoides are *I. pedunculosa* Miq., *I. rockii* S. Y. Hu, *I. yunnanensis* Franchet, *I. kirinsanensis* Nakai, and *I. sugerokii* Maxim. *Ilex shennongjiaensis* has foliage and fruit that suggest close affinity with *I. sugerokii,* but it can be distinguished from that species by the larger pyrenes that are dorsally sulcate and striate; the larger, earlier-ripening, bright red, glossy, sweet fruit; the larger, sessile stigmas with flattened, conspicuously separate lobes; the larger calyces with shallow sinuses and glabrous lobes; the shorter pedicels that are dilated at both ends; the glabrous peduncles bearing longer, eciliate prophylls; the shorter, glabrous, deciduous stipules; and the deeply grooved, shorter petioles.

The short, strongly grooved petioles of *Ilex shennongjiaensis* are also reminiscent of *I. kirinsanensis,* endemic to Mt. Kirin-san in Japan. Most of the features that distinguish *I. shennongjiaensis* from *I. sugerokii* also apply to and separate *I. kirinsanensis.* The lower surfaces of the leaves of *I. kirinsanensis* are described as being glandular-punctate. After more material is studied, this taxon might realistically be relegated to infraspecific rank within *I. sugerokii.*

Loesener (1901) tentatively assigned a Chinese collection, *Farges 129,* from Jiangkouzhen ("Tschen-keow-tin"), Sichuan Province, to *Ilex sugerokii* forma *brevipedunculata* Maxim. (= var. *brevipedunculata* (Maxim.) S. Y. Hu), commenting that it was intermediate between that form and *I. yunnanensis.* Hu (1949) regarded *Farges 129* as *I. yunnanensis* var. *gentilis* (Franchet) Loes. ex Diels.

Ilex wilsonii Loes.
2031 (A, CM, HIB, NA, NAS, PE).

Ilex yunnanensis Franchet var. *gentilis* (Franchet) Loes. ex Diels*, Bot. Jahrb. Syst. **29:** 435. 1900; Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. **78:** 132. 1901.
646 (A, HIB, PE); *891* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1303* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1763* (A, HIB, KUN, NA, NAS, NY, PE, UC); *1773* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

CELASTRACEAE

Celastrus angulatus Maxim.
1012 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1646* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Celastrus gemmatus Loes.
785 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC); *1220* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Celastrus glaucophyllus Rehder & Wilson (syn.: *C. rugosus* Rehder & Wilson)
193 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *313* (A, HIB, KUN, NA, PE, UC); *894* (A, HIB, KUN, NA, NAS, NY, PE, UC).

Celastrus orbiculatus Thunb.
690 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1006* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Celastrus rosthornianus Loes.
1282 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Euonymus acanthocarpus Franchet
574 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC).

Euonymus alatus (Thunb.) Sieb.
131 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *347* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *516* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *795* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1152* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1284* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Euonymus cornutus Hemsley
608 (A, HIB, NY, PE); *639* (A, CM, HIB, KUN, NA, NAS, PE); *865* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1289* (A, HIB).

Euonymus crinitus Pampan. (syn.: *E. elegantissimus* Loes. & Rehder)
1333 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus fortunei (Turcz.) Hand.-Mazz.
1337 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus giraldii Loes.*
261 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus hamiltonianus Wallich
137 (A, CM, HIB, NAS, NY, PE); *1023* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1054* (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC); *1233* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1552* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1749* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus kiautschovicus Loes.
2075 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus maackii Rupr.*
887 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus oxyphyllus Miq.
1288 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus phellomanes Loes.
366 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *954* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus porphyreus Loes.
864 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *965* (A, CM, HIB, KUN, PE, UC).
Euonymus sanguineus Loes.
1004 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1799* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1871* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus verrucosoides Loes.
1527 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Euonymus verrucosoides Loes. var. *viridiflora* Loes. & Rehder*, Pl. Wilsonianae **1**: 493. 1913.
398 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Microtropis triflora Merr. & Freeman
2018 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Perrottetia racemosa (Oliver) Loes.*
561 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1902* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

STAPHYLEACEAE

Euscaphis japonica (Thunb.) Kanitz
1942 (A, HIB).
Staphylea bumalda DC.
716 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Staphylea holocarpa Hemsley
6 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1084* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

ICACINACEAE

Hosiea sinensis (Oliver) Hemsley & Wilson
1082 (A, HIB, KUN, NAS, NY, PE, SFDH, UC).

ACERACEAE

Acer amplum Rehder
738 (A, CM, HIB, KUN, NA, NAS, PE).

Acer caudatum Wallich var. *multiserratum* (Maxim.) Rehder in Sarg. Trees Shrubs **1:** 163. 1905.
110 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *161* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

According to Bean (Trees Shrubs Hardy Brit. Isles. ed. 8. **1:** 220. 1970), the correct name of *Acer caudatum* Wallich is *A. papilio* King, the former name constituting a nomen ambiguum. Moreover, var. *multiserratum* is treated in the same work (**1:** 239) as a distinct species, *A. multiserratum* Maxim.; we have been unable to locate a proposal to treat this taxon at the varietal rank under *A. papilio.* Inasmuch as this problem is both taxonomic and nomenclatural, the varietal combination is not proposed here pending additional study of the taxonomy of the group, and the name is provisionally maintained as *Acer caudatum* var. *multiserratum.*

Acer davidii Franchet
517 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *536* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *679* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1125* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Acer erianthum Schwerin
1041 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1531* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1781* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Acer flabellatum Rehder
1127 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Acer franchetii Pax
83 (A, HIB); *1024* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1240* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1761* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1828* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Acer griseum (Franchet) Pax
1482 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1571* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1747* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Acer henryi Pax
1740 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Acer maximowiczii Pax
368 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *898* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Acer mono Maxim.
150 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Acer robustum Pax
1359 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Acer sinense Pax
1805 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Acer stachyophyllum Hiern
302 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1018* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1211* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Acer sutchuenense Franchet*
222 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Dipteronia sinensis Oliver
1063 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

SABIACEAE

Meliosma beaniana Rehder & Wilson
1007 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Meliosma dilleniifolia (Wallich ex Wight & Arnott) Walp. subsp. *cuneifolia* (Franchet) Beus. Blumea **19:** 442. 1971.
212 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1198* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1868* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Meliosma dilleniifolia (Wallich ex Wight & Arnott) Walp. subsp. *flexuosa* (Pampan.) Beus.* Blumea **19:** 444. 1971.
1100 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1949* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Meliosma veitchiorum Hemsley
1498 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

BALSAMINACEAE

Impatiens blephorosepala Pritzel ex Diels*
1246 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Impatiens dicentra Franchet
55 (A, CM, HIB, KUN, NAS, NY, PE, UC); *560* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *601* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *858* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Impatiens cf. *exiguiflora* Hooker f.
1960 (A, CM, HIB, KUN, NAS, NY, PE, UC).
Impatiens pterosepala Pritzel ex Diels
58 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *77* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *559* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *766* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1003* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1037* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Impatiens siculifera Hooker f.*
1090 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Impatiens stenosepala Pritzel ex Diels
558 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Impatiens sutchuanensis Franchet ex Hooker f.*
17 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *51* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

RHAMNACEAE

Berchemia flavescens (Wallich) Brongn.
1539 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1798* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Berchemia floribunda (Roxb.) Brongn.
737 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhamnus crenatus Sieb. & Zucc.
771 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1194* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1488* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1702* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1880* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhamnus davuricus Pallas
2024 (A, HIB, NA, PE).
Rhamnus dumetorum Schneider*
1628 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhamnus esquirolii Lévl.*
1683 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhamnus iteinophyllus Schneider
1019 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1047* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhamnus leptophyllus Schneider
508 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *522* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *628* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *629* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1021* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1336* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhamnus utilis Dcne.
465 (A, HIB); *1327* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1419* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1541* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

VITACEAE

Ampelopsis megalophylla Diels & Gilg
1354 (A, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cayratia oligocarpa (Lévl. & Vaniot) Gagnep.*
1542 (A, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cayratia pseudotrifolia W. T. Wang
474 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1494* (A, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1697* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Parthenocissus henryana (Hemsley) Diels & Gilg
1694 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Parthenocissus himalayana (Royle) Planchon
1036 (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Tetrastigma hemsleyanum Diels & Gilg
2010 (A, CM, HIB, NAS, PE, UC).
Tetrastigma obtectum Planchon
1621 (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC).
Tetrastigma obtectum (Wallich) Planchon var. *pilosum* Gagnep. Notul. Syst. Paris **1**: 323. 1911.
1596 (A, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Vitis betulifolia Diels & Gilg*
192 (A, HIB, NAS, PE, UC); *231* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *334* (A, HIB, KUN, NA, NAS, NY, PE, UC); *1313* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Vitis piasezkii Maxim. var. *pagnuccii* (Romanet ex Planchon) Rehder, J. Arnold Arbor. **3**: 223. 1922.
226 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *650* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1049* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1345* (A, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1355* (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1734* (A, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

TILIACEAE

Grewia biloba D. Don
1647 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Tilia chinensis Maxim.
395 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1307* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1319* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1533* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Tilia oliveri Szysz. var. *cinerascens* Rehder & Wilson, Pl. Wilsonianae **2**: 367. 1915.
1119 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1120* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

ACTINIDIACEAE

Actinidia callosa Lindley*
473 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1710* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Actinidia callosa Lindley var. *henryi* Maxim. Trudy Imp. S.-Petersburgsk. Bot. Sada **11**: 36. 1890.
249 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Actinidia chinensis Planchon
469 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *749* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *806* (A, HIB).

Actinidia chinensis Planchon var. *hispida* C. F. Liang, Acta Phytotax. Sinica **13:** 33. 1975.
237 (HIB).
Actinidia polygama (Sieb. & Zucc.) Maxim.
74 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Actinidia polygama (Sieb. & Zucc.) Maxim. var. *lecomtei* (Nakai) H. L. Li, J. Arnold Arbor. **33:** 22. 1952.
339 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Actinidia tetramera Maxim.
839a (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Clematoclethra cf. *franchetii* Komarov
872 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Clematoclethra hemsleyi Baillon
640 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *944* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1532* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Clematoclethra lanosa Rehder*
1752 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

THEACEAE

Camellia cuspidata (Kochs) Veitch
801 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *2037* (A, HIB, NA, NAS, PE, UC).
Eurya alata Kobuski
1447 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1489* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Eurya brevistyla Kobuski
521 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Eurya loquaiana Dunn
2028 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Eurya obtusifolia Chang
2004 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Stewartia sinensis Rehder & Wilson
1504 (A, CM, HIB, NY, PE); *1568* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

GUTTIFERAE

Hypericum ascyron L.
363 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *791* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Hypericum cf. *attenuatum* Choisy
108 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Hypericum patulum Thunb.
2021 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Hypericum perforatum L.
396 (A, HIB, KUN, NAS, NY, PE, UC); *1050* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

VIOLACEAE

Viola grypoceras A. Gray var. *pubescens* Nakai*, Bot. Mag. Tokyo **36:** 55, 89. 1922.
1502 (A, HIB).
Viola prionantha Bunge
1645 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).
Viola stewardiana W. Becker
1493 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

FLACOURTIACEAE

Carrierea calycina Franchet
245 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

STACHYURACEAE

Stachyurus chinensis Franchet
554 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1078* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1424* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Stachyurus chinensis Franchet var. *latus* H. L. Li, Bull. Torrey Bot. Club **70:** 627. 1943.
130 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *194* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *600* (A, HIB, KUN, NAS, NY, PE, SFDH, UC, WH); *1128* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

BEGONIACEAE

Begonia evansiana Andrews
493 (A, HIB).
Begonia sinensis A. DC.
498 (A, HIB, KUN, NA, PE, UC); *1642* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Begonia sp.
2012 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

ELAEAGNACEAE

Elaeagnus henryi Warb.
2077 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Elaeagnus lanceolata Warb.
95 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *145* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *227* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *459* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1030* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Elaeagnus umbellata Thunb.
1182 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1196* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

LYTHRACEAE

Rotala indica (Willd.) Koehne
2084 (A, HIB).

NYSSACEAE

Davidia involucrata Baillon var. *vilmoriniana* (Dode) Wangerin in Engler, Pflanzenr. IV. **220a**(Heft 41): 19. 1910.
1473 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

ALANGIACEAE

Alangium chinense (Lour.) Harms
452 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1601* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1631* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Alangium platanifolium (Sieb. & Zucc.) Harms
604 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1738* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Alangium sinicum (Nakai) S. Y. Hu, Spongberg, & Z. Cheng, comb. nov.*
BASIONYM: *Marlea sinica* Nakai, Fl. Sylv. Koreana **17:** 29. 1928.
1017 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1096* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1703* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Two species of *Alangium, A. chinense* (Lour.) Harms and *A. platanifolium* (Sieb. & Zucc.) Harms, have been credited to the Shennongjia Forest District (Anonymous, 1980) and Hubei Province (Bloembergen, 1939, *map* on p. 163). Our field activities confirmed the presence of these species in the Shennongjia area but also revealed a third taxon that appeared distinct from both *A. chinense* and *A. platanifolium.* Subsequent studies and a comparison of the Shennongjia collections with specimens in the Harvard University Herbaria confirm this third taxon, which (based on specimens at A and GH) is not confined to western Hubei but is widely distributed in China in Shaanxi, Shandong, Shanxi, Henan, Jiangsu, Hubei, Guizhou, and Yunnan provinces.

S. Y. Hu, in earlier unpublished studies utilizing specimens at A and GH, also recognized this third species and stated that Nakai (1928) had provided it with a name under the genus *Marlea.* The appropriate new combination under *Alangium* is made here. The following key, based primarily on specimens collected from western Hubei but supplemented by other Chinese specimens, will aid in distinguishing the three species.

Key to the Species of *Alangium* in the Shennongjia Forest District

1. Peduncles 1.3–1.6 cm long; pedicels 1.3–1.6 mm long; corollas 0.8–1.9 cm long; styles pubescent.
   2. Ovaries and fruits 1-celled; branchlets and petioles sparingly pubescent, leaf surfaces glabrous except for tufts of hairs in vein axils. . . . . *A. sinicum.*

2. Ovaries and fruits 2-celled; branchlets, petioles, and leaf surfaces pubescent. . . . . *A. chinense.*
1. Peduncles 3.2–3.5 cm long; pedicels 2–3.8 cm long; corollas 2.8–3.7 cm long; styles glabrous. . . . . *A. platanifolium.*

ONAGRACEAE

Circaea alpina L. subsp. *imaicola* (Ascherson & Magnus) Kitamura, Fl. Afghanistan, 279. 1960.
28 (A, HIB).

Circaea erubescens Franchet & Sav.
850 (A, CM, E, HIB, KUN, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Circaea glabrescens (Pampan.) Hand.-Mazz.*
133 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *419* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Circaea mollis Sieb. & Zucc.
851 (A, CM, HIB, PE); *1636* (A, CM, HIB, KUN, NA, PE).

Circaea repens Wallich ex Ascherson & Magnus*
1157 (A, CM, E, HIB, KUN, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Epilobium cephalostigma Hausskn.
85 (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *119* (A, CM, HIB, KUN, NA, NAS, PE, UC).

Epilobium aff. *nepalense* Hausskn.*
318 (A, CM, HIB, KUN, NA, NAS, NY, PE).

Epilobium parviflorum Schreber
1161 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1832* (A, CM, E, HIB, KUN, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Epilobium sinense Lévl.*
24 (A, HIB, KUN, NAS, PE); *319* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *380* (A, HIB, NAS, NY, PE, UC); *599* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *722* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1013* (A, CM, HIB, KUN, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1831* (A, CM, E, HIB, KUN, MO, NA, NAS, NY, PE, SFDH, UC, WH).

ARALIACEAE

Acanthopanax giraldii Harms
115 (A, CM, E, HIB, NAS, PE, UC); *160* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Acanthopanax henryi (Oliver) Harms
1195 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1338* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Acanthopanax leucorrhizus (Oliver) Harms var. *fulvescens* Harms & Rehder, Pl. Wilsonianae **2:** 558. 1916.
185 (A, CM, HIB, KUN, NY, PE, UC); *367* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *905* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1392* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Acanthopanax leucorrhizus (Oliver) Harms var. *scaberulus* Harms & Rehder, Pl. Wilsonianae **2:** 558. 1916.
975 (A, HIB, NY, PE, UC).
Acanthopanax setchuenensis Harms ex Diels
109 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *219* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1129* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1757* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1797* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Acanthopanax trifoliatus (L.) Merr.
1102 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Aralia chinensis L.
636 (A, HIB); *1123* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Aralia echinocaulis Hand.-Mazz.*
381 (A, CM, HIB, NA, NY, PE, UC).
Hedera nepalensis K. Koch var. *sinensis* (Tobler) Rehder, J. Arnold Arb. **4:** 250. 1923.
702 (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH); *1083* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Nothopanax davidii (Franchet) Harms ex Diels
299 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *675* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1015* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1088* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1627* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *2042* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Panax pseudo-ginseng Wallich (intermediate between vars. *bipinnatifidus* (Seem.) H. L. Li (Sargentia **2:** 118. 1942) and *japonicus* (C. A. Meyer) Hoo & Tseng)
314 (A, HIB).
Panax pseudo-ginseng Wallich var. *japonicus* (C. A. Meyer) Hoo & Tseng, Acta Phytotax. Sinica **11:** 437. 1973.
1803 (A, HIB, NAS, NY, PE).

UMBELLIFERAE

Angelica pubescens Maxim.
1487 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Angelica sp.
256 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1580* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Bupleurum chinense DC.
1641 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Bupleurum longicaule Wallich ex DC. var. *franchetii* H. Boiss. Bull. Soc. Bot. France **53:** 425. 1906.
1224 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Bupleurum longicaule Wallich ex DC. var. *giraldii* Wolff* in Engler, Pflanzenr. IV. **228**(Heft 43): 123. 1910.
111 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *254* (A, CM, E,

HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *949* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Bupleurum longiradiatum Turcz. var. *porphyranthum* Shan & Y. Li, Acta Phytotax. Sinica **12:** 270. 1974.

404 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *903* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1213* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Bupleurum petiolatum Franchet*

564 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cryptotaenia japonica Hassk. (syn.: *C. canadensis* (L.) DC. var. *japonica* (Hassk.) Makino, Bot. Mag. Tokyo **22:** 175. 1908.)

424 (A, HIB); *549* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Heracleum acuminatum Franchet*

1774 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC); *1810* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Heracleum moellendorffii Hance*

1253 (A, HIB, NA, NAS, PE, UC); *1813* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Heracleum yungningense Hand.-Mazz.

1254 (A, HIB).

Ligusticum daucoides Franchet*

948 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Ligusticum sinense Oliver

116 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *138* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1811* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Melanosciadum pimpinelloideum H. Boiss.*

417 (A, HIB, NY, PE, UC); *686* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC); *1076* (A, HIB, NAS, NY, PE, UC); *1814* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Nothosmyrnium japonicum Miq. var. *sutchuensis* H. Boiss.* Bull. Soc. Bot. France **61:** 349. 1909.

654 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY; PE, SFDH, UC, WH); *1201* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1242* (A, CM, HIB, KUN, NAS, PE, UC).

Oenanthe dielsii H. Boiss.

1458 (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC).

Peucedanum praeruptorum Dunn

140 (HIB); *464* (A, HIB, PE, UC).

Pimpinella arguta Diels

569 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1252* (A, HIB).

Pimpinella diversifolia DC.

146 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Pimpinella diversifolia DC. var. *stolonifera* Hand.-Mazz.* Symb. Sinicae **7:** 714. 1933.

699 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Pleurospermum giraldii Diels*
178 (A, HIB, PE, UC).
Sanicula orthacantha S. Moore
506 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

CORNACEAE

Aucuba chinensis Bentham*
615 (A, HIB, NA); *1676* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1756* (A, CM, HIB, KUN, NAS, NY, PE, UC); *1901* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, WH).
Cornus chinensis Wangerin (syn.: *Macrocarpium chinense* (Wangerin) Hutch.)
1696 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cornus controversa Hemsley
19 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *644* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1014* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cornus kousa Hance (syn.: *Dendrobenthamia japonica* (DC.) Fang var. *chinensis* (Osborn) Fang, Acta Phytotax. Sinica **2:** 105. 1953.)
224 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *784* (A, HIB); *1244* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1316* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cornus kousa Hance var. *angustata* Chun, Sunyatsenia **1:** 285. 1934. (syn.: *Dendrobenthamia angustata* (Chun) Fang, Acta Phytotax. Sinica **2:** 95. 1953.)
2032 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cornus macrophylla Wallich
369 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *883* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Cornus paucinervis Hance
1629 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Helwingia chinensis Batalin
453 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1897* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH).
Helwingia japonica (Thunb.) Dietr. var. *japonica*
195 (A, CM, HIB, KUN, NA, NAS, NY, PE); *355* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Helwingia japonica (Thunb.) Dietr. var. *hypoleuca* Hemsley ex Rehder, Pl. Wilsonianae **2:** 570. 1916.
1071 (A, HIB, PE, UC).
Helwingia japonica (Thunb.) Dietr. (intermediate between vars. *japonica* and *hypoleuca*)
862 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

CLETHRACEAE

Clethra fargesii Franchet
485 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *773* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1276* (A, CM, HIB, KUN, NA,

NAS, NY, PE, SFDH, UC, WH); *1469* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

PYROLACEAE

Chimaphila japonica Miq.
912 (A, HIB).
Monotropa hypopithys L.
867 (A, CM, HIB, NAS, NY, PE, UC).
Pyrola decorata Andres
1250 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

ERICACEAE

Enkianthus chinensis Franchet
626 (HIB); *718* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1132* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1311* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Enkianthus serrulatus (Wilson) Schneider
2014 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Lyonia ovalifolia (Wallich) Drude var. *elliptica* (Sieb. & Zucc.) Hand.-Mazz. Symb. Sinicae 7(4): 788. 1936.
1394 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Pieris formosa (Wallich) D. Don
769 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1474* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Rhododendron argyrophyllum Franchet subsp. *hypoglaucum* (Hemsley) Chamberlain, Notes Roy. Bot. Gard. Edinburgh **37**: 329. 1979.
609 (A, HIB, KUN, NAS, NY, PE, SFDH, UC, WH); *1322* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1758* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhododendron augustinii Hemsley
578 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *739* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC); *1748* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1780* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhododendron concinnum Hemsley
875 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhododendron fargesii Franchet
124 (A, HIB, KUN, NA, NAS, PE, UC); *942* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhododendron fortunei Lindley subsp. *discolor* (Franchet) Chamberlain, Notes Roy. Bot. Gard. Edinburgh **37**: 330. 1979.
2040 (A, HIB).
Rhododendron maculiferum Franchet
123 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *863* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *943* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Rhododendron mariesii Hemsley & Wilson
787 (A, HIB, PE).
Rhododendron micranthum Turcz.
208 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Rhododendron simsii Planchon
774 (A, HIB); *1425* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1932* (A, HIB, PE).
Rhododendron sutchuenense Franchet
1231 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Vaccinium henryi Hemsley
1497 (A, CM, E, HIB, KUN, KYO, NAS, NY, PE, SFDH, UC, WH).
Vaccinium japonicum Miq. var. *sinicum* (Nakai) Rehder, J. Arnold Arbor. **5**: 56. 1924. (syn.: *Hugeria vaccinioides* (Lévl.) Hara)
730 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1475* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

MYRSINACEAE

Ardisia crenata Sims
1455 (A, HIB); *1620* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1677* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Ardisia japonica (Thunb.) Blume
1926 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH).
Myrsine africana L.
479 (A, HIB, NA, NY, PE).

PRIMULACEAE

Androsace henryi Oliver
1456 (HIB).
Lysimachia christinae Hance
359 (A, HIB).
Lysimachia clethroides Duby
727 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1503* (A, HIB, NA, NAS, NY, PE, UC).
Lysimachia congestiflora Hemsley
1093 (A, HIB, KUN, NA, NAS, NY, PE, UC).
Lysimachia stenosepala Hemsley
200 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *570* (A, HIB, PE, UC).
Primula ovalifolia Franchet
1472 (A, CM, HIB, NA, NAS, PE, UC).

EBENACEAE

Diospyros lotus L.
1478 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1605* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

SYMPLOCACEAE

Symplocos anomala Brand*
1693 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Symplocos lancifolia Sieb. & Zucc.
2019 (A, CM, HIB, PE).
Symplocos paniculata (Thunb.) Miq.
744 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1217* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1530* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1851* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH); *1886* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC).

STYRACACEAE

Styrax hemsleyana Diels*
348 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1133* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1390* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Styrax japonica Sieb. & Zucc.
763 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1484* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

OLEACEAE

Forsythia suspensa (Thunb.) Vahl
694 (HIB); *1707* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Fraxinus paxiana Lingelsh.*
1538 (A, CM, HIB, PE).
Jasminum floridum Bunge
1606 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Jasminum lanceolarium Roxb.
1440 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1910* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Jasminum urophyllum Hemsley
2078 (A, HIB, KUN, NA, NY, PE, UC).
Ligustrum acutissimum Koehne
242 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *340* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1031* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1216* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Ligustrum henryi Hemsley
1911 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Ligustrum obtusifolium Sieb. & Zucc.*
1735 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Ligustrum quihoui Carrière
1444 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Osmanthus armatus Diels
691 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *692* (A, HIB).

Osmanthus fragrans Lour.* (collected from a plant in cultivation)
1575 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Syringa reflexa Schneider*
264 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *908* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *955* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

LOGANIACEAE

Buddleja albiflora Hemsley
257 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Buddleja davidii Franchet
671 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1418* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

GENTIANACEAE

Gentiana panthaica Burkill*
170 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Gentianopsis scabromarginata (H. Sm.) Ma
34 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Halenia elliptica D. Don var. *elliptica*
267 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *871* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Halenia elliptica D. Don var. *grandiflora* Hemsley, J. Linn. Soc., Bot. **26:** 141. 1890.
683 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *856* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1215* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Lomatogonium bellum (Hemsley) H. Sm.*
174 (A, CM, HIB, KUN, NY, PE, SFDH, UC); *946* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Swertia bimaculata (Sieb. & Zucc.) Hooker & Thomson
180 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *228* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *317* (A, CM, HIB, KUN, NAS, NY, PE, UC); *1958* (A, CM, HIB, NY, PE).
Swertia punicea Hemsley*
1595 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).
Swertia tetragona Edgew.*
1850 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Collection no. *1850* was mistakenly distributed as *Swertia punicea*; the two plants are quite different.

Tripterospermum affine (Wallich) H. Sm.
39 (A, CM, HIB, NAS, NY, PE); *143* (A, CM, HIB, KUN, PE, UC); *566* (A, HIB, NA, PE); *1927* (A, CM, HIB, NA, NAS, NY, PE).

ASCLEPIADACEAE

Cynanchum auriculatum Royle ex Wight
1225 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cynanchum inamoenum (Maxim.) Loes.
634 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Metaplexis hemsleyana Oliver (syn.: *M. sinensis* (Hemsley) Hu)
439 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1420* (A, CM, HIB, NAS, NY, PE); *1649* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

CONVOLVULACEAE

Cuscuta japonica Choisy
1045 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1570* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Porana racemosa Roxb.
1443 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

BORAGINACEAE

Cynoglossum zeylanicum (Vahl) Thunb.
379 (A, HIB, NAS, NY, PE, UC); *790* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

VERBENACEAE

Callicarpa bodinieri Lévl. var. *bodinieri*
408 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1681* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *2007* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *2060* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *2080* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Callicarpa bodinieri Lévl. var. *giraldii* (Hesse ex Rehder) Rehder, J. Arnold Arbor. **15:** 322. 1934.
846 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Caryopteris incana (Thunb.) Miq.
1656 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Clerodendrum bungei Steudel
1928 (A, CM, HIB, NAS, PE, UC).
Clerodendrum trichotomum Thunb. var. *trichotomum*
401 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *602* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1878* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Clerodendrum trichotomum Thunb. var. *fargesii* (Dode) Rehder, Pl. Wilsonianae **3:** 376. 1916.
848 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

LABIATAE

Clinopodium polycephalum (Vaniot) C. Y. Wu & Hsuan*, Observ. Fl. Hwangshanicum, 168. 1965 (citation incorrect in Index Kewensis).
1968 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Elsholtzia ciliata (Thunb.) Hylander
1135 (A, HIB, KUN, NA, NY, PE); *1518* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1962* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Elsholtzia cypriani (Pampan.) S. Chow*, Observ. Fl. Hwangshanicum, 170. 1965 (citation incorrect in Index Kewensis).
1685 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Elsholtzia flava Bentham
1945 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Elsholtzia fruticosa (D. Don) Rehder
220 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1746* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Kinostemon ornatum (Hemsley) Kudo (syn.: *Teucrium ornatum* Hemsley)
420 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Leonurus artemisia (Lour.) S. Y. Hu (incl. *L. japonicus* Hylander)
746 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Mosla scabra (Thunb.) C. Y. Wu & H. W. Li
1965 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Origanum vulgare L.
568 (A, HIB, NA, PE); *866* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Phlomis umbrosa Turcz.
113 (A, HIB, KUN, NA, PE, UC); *352* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1866* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rabdosia excisoides (Sun ex C. H. Hu) C. Y. Wu & H. W. Li
142 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *206* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rabdosia nervosa (Hemsley) C. Y. Wu & H. W. Li
1351 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Salvia maximowicziana Hemsley
182 (A, CM, HIB, KUN, NA, NAS, PE, UC); *376* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

SOLANACEAE

Lycianthes lysimachioides (Wallich) Bitter
617 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Physalis alkekengi L. var. *franchetii* (Mast.) Makino, Bot. Mag. Tokyo **22**: 34. 1908.
475 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1550* (A, HIB, NY, PE).
Scopolia sinensis Hemsley (syn.: *Atropanthe sinensis* (Hemsley) Pascher)
483 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Solanum lyratum L.
1576 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Solanum nigrum L.
429 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Solanum pittosporifolium Hemsley
1278 (A, CM, HIB, NA, NAS, PE).

SCROPHULARIACEAE

Hemiphragma heterophyllum Wallich*
166 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Melampyrum roseum Maxim. var. *obtusifolium* (Bonati) Hong, Fl. Reip. Pop. Sinicae **67**(2): 367. 1979.
1853 (A, CM, E, HIB, KUN, KYO, NA, NAS, PE, SFDH, UC, WH).
Mimulus tenellus Bunge
1770 (A, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Pedicularis holocalyx Hand.-Mazz.
78 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Pedicularis resupinata L.
567 (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1214* (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Pedicularis torta Maxim.
169 (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH); *259* (A, HIB, KUN, NA, NAS, NY, PE, UC); *868* (A, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Scrophularia henryi Hemsley*
177 (A, HIB, PE).
Veronicastrum caulopterum (Hance) Yamazaki
2008 (A, HIB, KUN, NA, NY, PE, UC).
Unidentified Scrophulariaceae
169a (A).

OROBANCHACEAE

Orobanche coerulescens Stephan
901 (HIB).

GESNERIACEAE

Hemiboea subcapitata C. B. Clarke
407 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Lysionotis pauciflorus Maxim.
755 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1705* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Paraboea sinensis (Oliver) B. L. Burtt*, Notes Roy. Bot. Gard. Edinburgh **38**: 471. 1980.
1715 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

ACANTHACEAE

Asystasiella chinensis (S. Moore) E. Hossain
1680 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

PHRYMACEAE

Phryma leptostachya L. var. *asiatica* Hara, Enum. Spermatophyt. Jap. **1:** 297. 1948.
762 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

RUBIACEAE

Anotis hirsuta (L. f.) Boerl.
2006 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Emmenopterys henryi Oliver
243 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Leptodermis aff. *oblonga* Bunge
1700 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Collection no. *1700* is tentatively assigned to *Leptodermis oblonga* Bunge. There appears to be considerable confusion concerning the Chinese species, especially with regard to fruiting material, and the genus is in need of careful study both in the field and in the herbarium.

Leptodermis wilsonii Hort. ex Diels*
581 (A, HIB, KUN, NA, PE, UC).
Ophiorrhiza japonica Blume
509 (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH); *1087* (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC, WH); *1449* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Paederia scandens (Lour.) Merr.
511 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1072* (A, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rubia cordifolia L.
1306 (A, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

CAPRIFOLIACEAE

Abelia engleriana (Graebner) Rehder
76 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *653* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Abelia sp.
1741 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Dipelta floribunda Maxim.
1611 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1684* (A, HIB).
Lonicera gynochlamydea Hemsley
68 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *225* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *411* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *642* (A, HIB, NA, NAS, PE, UC); *680* (A, CM, E, HIB, KUN,

NA, NAS, NY, PE, SFDH, UC, WH); *1040* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1073* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1281* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1467* (HIB); *1762* (A, CM, HIB, NA, NAS, PE); *1825* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lonicera henryi Hemsley*

240 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *342* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *612* (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC, WH); *736* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1046* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1095* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lonicera japonica Thunb.

443 (A, HIB).

Lonicera koehneana Rehder

315 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *345* (A, HIB, NA, PE); *394* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *907a* (A, NA, UC); *1802* (A, HIB, PE, UC).

Collection no. *907a* was distributed as *Lonicera koehneana* Rehder var. *longipes* Rehder. This name was apparently never published; there is no type at A, and the single specimen bearing this name was not determined by Rehder. Moreover, the varietal name does not appear in Rehder's published writings on *Lonicera.*

Lonicera longa Rehder*

260 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Lonicera maackii Maxim.

441 (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *471* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1442* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1452* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1584* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1612* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lonicera nervosa Maxim.

157 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *966* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Lonicera cf. *nervosa* Maxim.

251 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lonicera pileata Oliver

705 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1099* (A, HIB, NA, NAS, PE, UC); *1908* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1941* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lonicera similis Hemsley

1426 (A, HIB, NY, PE, UC).

Lonicera taksienensis Franchet

976 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Lonicera tangutica Maxim.

907 (A).

Collection no. *907* represents a mixed collection, part of which (no. *907a*) is *Lonicera koehneana* Rehder. The identity and the distribution of the specimens in Chinese herbaria are not known.

Lonicera tragophylla Hemsley

611 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Lonicera trichopoda Franchet*

1743 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Sambucus adnata Wallich ex DC.* (syn.: *S. schweriniana* Rehder)

38 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Sambucus chinensis Lindley

1108 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Triosteum himalayanum Wallich

50 (A, HIB, NA, NAS, NY, PE, UC); *175* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *970* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum betulifolium Batalin

557 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1043* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1098* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1415* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum cylindricum Buch.-Ham. ex D. Don

445 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1414* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1930* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Viburnum erubescens Wallich

32 (A, CM, HIB, KUN, NA, NAS, PE, UC); *947* (A, HIB, NA, PE).

Viburnum flavescens W. W. Sm.*

1035 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Viburnum foetidum Wallich var. *rectangulatum* (Graebner) Rehder* in Sargent, Trees Shrubs **2:** 114. 1908.

1411 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *2002* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum formosanum (Maxim.) Hayata*

434 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum hupehense Rehder subsp. *hupehense**

14 (A, HIB, NA, PE); *73* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *190* (A, HIB, NA, PE); *241* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *390b* (A; see *V. lobophyllum* for note on distribution of this collection); *607* (A, HIB); *630* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1199* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1325* (A, HIB, NA, NY, PE); *1577* (A, HIB, NA, NAS, PE, UC); *1733* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1766b* (A, NA).

Collection no. *1766* represents a mixed collection, part of which (*1766a*) is *Viburnum ovalifolium* Rehder. The identity and the distribution of the specimens in Chinese herbaria are unknown.

Viburnum hupehense Rehder subsp. *septentrionale* Hsu*, Acta Phytotax. Sinica **11:** 77. 1966.

98 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC); *1286* (A, HIB, NA, NAS, PE).

Viburnum ichangense Rehder var. *ichangense*

1219 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1331* (A, CM, E, HIB,

KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1889a* (A, NA, NY); *2038* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum ichangense Rehder var. **atratocarpum** (Hsu) T. R. Dudley & S. C. Sun, comb. nov.*

BASIONYM. *Viburnum erosum* subsp. *ichangense* (Hemsley) P. S. Hsu var. *atratocarpum* P. S. Hsu, Acta Phytotax. Sinica **13**(1): 127. 1975.

446 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *775* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1889b–d* (A, CM, NA, UC).

Collection no. *1889* represents a mixed collection, part of which (*1889a*) is *Viburnum ichangense* Rehder var. *ichangense*. The identity and the distribution of the collections in China are not known.

Viburnum lobophyllum Graebner*

250 (A, CM, HIB, KUN, NA, NAS, NY, PE); *390a* (A, CM, NA, NY, PE, UC); *874* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1416* (A, HIB, KUN, NA, NAS, NY, PE, UC).

Collection no. *390* represents a mixed collection and was renumbered *390a* and *390b* (*Viburnum hupehensis* subsp. *hupehensis*). The identity and the distribution of the sheets in Chinese herbaria, other than the sheet at PE, are not known; however, HIB, KUN, NAS, SFDH, and WH all received specimens under no. *390*.

Viburnum ovatifolium Rehder

1124 (A, CM, HIB, KUN, NA, PE, SFDH, UC); *1766a* (A, CM, NA, NY, WH); *1888* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum plicatum Thunb. forma *tomentosum* (Thunberg) Rehder, J. Arnold Arb. **26:** 77. 1945.

1658 (A, HIB).

Viburnum propinquum Hemsley

462 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1069* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1413* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1701* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1904* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum rhytidophyllum Hemsley

82 (A, HIB); *152* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *210* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *649* (A, HIB, NA, PE); *1002* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum sargentii Koehne

726 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1226* (A, CM, HIB, KUN, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1536* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1730a* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1730b* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC, WH).

Viburnum setigerum Hance

1247 (A, HIB); *1335* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1887* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1963* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *2043* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum sympodiale Graebner

1209 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1287* (A, CM, HIB,

KUN, NA, NAS, NY, PE, UC); *1334* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Viburnum utile Hemsley

1412 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1581* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1618* (A, CM, HIB, NA, NAS, NY, PE).

Viburnum veitchii C. H. Wright*

374 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *861* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1052* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Weigela japonica Thunb. var. *sinica* (Rehder) Bailey, Gentes Herb. **2:** 49. 1929.

460 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *750* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1951* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

VALERIANACEAE

Patrinia angustifolia Hemsley

81 (A, CM, HIB, PE).

Patrinia monandra C. B. Clarke

25 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *573* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC); *755a* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1222* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

DIPSACACEAE

Dipsacus asper Wallich

756 (A, CM, HIB, NAS, NY, PE, UC).

Dipsacus japonicus Miq.

2 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *64* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Triplostegia glandulifera Wallich

1349 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

CUCURBITACEAE

Gynostemma cardiospermum Cogn. ex Oliver (distributed as *Gynostemma pentaphyllum* (Thunb.) Makino, which has free or only slightly united filaments; our specimens have united filaments)

538 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Hemsleya chinensis Cogn. ex Forbes & Hemsley

490 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *641* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Schizopepon dioicus Cogn.

1034 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1251* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Thladiantha henryi Hemsley

62 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Thladiantha maculata Cogn.*

1323 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Thladiantha nudiflora Hemsley
637 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *794* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1477* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

CAMPANULACEAE

Adenophora axilliflora Borbas
3 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *52* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *335* (A, HIB, PE).
Adenophora capillaris Hemsley
60 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *201* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1122* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1154* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Adenophora wilsonii Nannf.
1280 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Campanula punctata Lam.
99 (HIB); *179* (HIB); *324* (A, HIB, NY, PE); *360* (A, CM, HIB, KUN, NA, NAS, PE, UC).
Campanumoea javanica Blume var. *japonica* (Maxim.) Makino, Bot. Mag. Tokyo **22:** 155. 1908. (syn.: *C. maximowiczii* Honda)
455 (A, HIB, NY, PE, UC, WH); *2009* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Codonopsis pilosula (Franchet) Nannf.
1057 (A, HIB).
Codonopsis tangshen Oliver
97 (A, HIB, KUN, NA, NAS, PE, UC); *186* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *234* (A, CM, HIB, KUN, NA, NY, PE, SFDH, UC); *1881* (A, CM, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Pratia nummularia (Lam.) A. Br. & Ascherson
1964 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

COMPOSITAE

Adenocaulon himalaicum Edgew.
548 (A, HIB, NA, NAS, NY, PE); *1042* (A, HIB, NY, PE, UC).
Ainsliaea gracilis Franchet
1970 (A, CM, HIB, NA, NAS, PE, UC); *2041* (A, HIB, NA, NY, PE, UC).
Ainsliaea triflora (Buch.-Ham.) Druce*
1598 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Anaphalis margaritacea (L.) Bentham & Hooker subsp. *japonica* (Sch.-Bip.) Kitamura, Acta Phytotax. Geobot. **5:** 148. 1936. (distributed as *A. margaritacea* var. *japonica* (Sch.-Bip.) Makino)
22 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Anaphalis sinica Hance
44 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *963* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Artemisia annua L.
757 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1567* (A, HIB, NAS, NY, PE, UC); *1643* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Artemisia argyi Lévl. & Vaniot
1520 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Artemisia argyi Lévl. & Vaniot var. *incana* (Maxim.) Pampan. Nuovo Giorn. Bot. Ital. **36**: 451. 1930.
1597 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Artemisia capillaris Thunb.
761 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Artemisia lactiflora Wallich
323 (A, CM, HIB, KUN, NA, NAS, PE, UC).
Artemisia subdigitata Mattf.
59 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Aster ageratoides Turcz. var. *ageratoides*
122 (A, HIB, NAS, NY, PE, UC); *1277* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Collection no. *122* was distributed as *A. ageratoides* var. *scaberulus* (Miq.) Ling, and collection no. *1277* as *A. ageratoides* var. *micranthus* Ling; both varietal names are unpublished.

Aster ageratoides Turcz. var. *laticorymbus* (Vaniot) Hand.-Mazz. Acta Horti Gothob. **12**: 214. 1938.
587 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *623* (A, CM, HIB, NA, NAS, NY, PE, SFDH, UC); *1857* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Aster albescens (DC.) Hand.-Mazz.
1061 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Aster brachyphyllus Chang*
1619 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Bidens parviflora Willd.
1662 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Bidens pilosa L.
1404 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1405* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Bidens tripartita L.
1256 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cacalia ainsliaeflora (Franchet) Hand.-Mazz. (syn.: *C. leucanthema* (Dunn) Ling)
1162 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Cacalia hastata L. var. *glabra* Ledeb. Fl. Altaica **4**: 52. 1833.
878 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Cacalia leucocephala (Franchet) Hand.-Mazz.
35 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cacalia profundorum (Dunn) Hand.-Mazz.
610 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Cacalia sinica Ling
1783 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cacalia tangutica (Franchet) Hand.-Mazz.
21 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *670* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Cacalia vespertilio (Franchet) Hand.-Mazz.*
1687 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Carpesium cernuum L.
689 (A, HIB, PE, UC).

Carpesium divaricatum Sieb. & Zucc.
535 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Carpesium faberi Winkler
487 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Chrysanthemum boreale (Makino) Makino* (syn.: *Dendranthema boreale* (Makino) Ling)
895 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1329* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1742* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Chrysanthemum indicum L. (syn.: *Dendranthema indica* (L.) Moulins)
132 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *959* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Cirsium fargesii (Franchet) Diels
54 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

Cirsium henryi (Franchet) Diels
938 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Cirsium lineare (Thunb.) Sch.-Bip. var. *intermedium* (Pampan.) Petrak, Repert. Spec. Nov. Regni Veg. **43:** 276. 1938.
740 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Conyza canadensis (L.) Cronq.
721 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Erigeron elongatus Ledeb.
33 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Eupatorium chinense L. (including *E. japonicum* Thunb.)
1229 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1519* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Galinsoga parviflora Cav.
431 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

Gynura crepidioides Bentham
489 (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC, WH).

Kalimeris indica (L.) Sch.-Bip.
1105 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Lactuca graciliflora (Wallich) DC.*
2017 (A, HIB, NY, PE).

Leontopodium japonicum Miq.
66 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *461* (A, CM, HIB, NAS, PE, UC); *701* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Ligularia hodgsonii Hooker
362 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Ligularia veitchiana (Hemsley) Greenman
1205 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Pertya sinensis Oliver
1537 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Picris hieracioides L. subsp. *japonica* (Thunb.) Krylov, Fl. Altai, 727. 1904.
121 (A, HIB, KUN, NA, NAS, NY, PE, UC); *354* (A, CM, HIB, KUN, NA, NAS, NY, PE, UC); *951* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Prenanthes tatarinowii Maxim.
681 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *968* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Rhynchospermum verticillatum Reinw.*
423 (A, HIB, PE, UC).
Saussurea cordifolia Hemsley
153 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1765* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Saussurea deltoides (DC.) C. B. Clarke*
1505 (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC, WH).
Saussurea silvestrii Pampan.
400 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Saussurea veitchiana Drumm. & Hutch.
162 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *953* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Saussurea sp.
1873 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Senecio scandens Buch.-Ham. ex D. Don
796 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *823* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Siegesbeckia pubescens Makino
480 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Solidago decurrens Lour.
1257 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *2016* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Synurus deltoides (Aiton) Nakai
1737 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Youngia denticulata (Houtt.) Kitamura (syn.: *Ixeris denticulata* (Houtt.) Stebbins)
1617 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

MONOCOTYLEDONES

GRAMINEAE

Agrostis clavata Trin., *s.l.**
1321 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Arthraxon hispidus (Thunb.) Makino
1402 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Arthraxon hispidus (Thunb.) Makino var. *cryptatherus* (Hackel) Honda*, Bot. Mag. Tokyo **39**: 277. 1925.
1655 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Dactylis glomerata L.
972 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Deschampsia caespitosa (L.) Beauv.
47 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Deyeuxia sylvatica (Schrader) Kunth*
392 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Digitaria sanguinalis (L.) Scop.
1471 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Erianthus fulvus Nees
1403 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Isachne nipponensis Ohwi
1959 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Melica onoei Franchet & Sav.
687 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Microstegium nudum (Trin.) A. Camus*
338 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1966* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Muhlenbergia hugelii Trin.*
725 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).
Oplismenus undulatifolius (Ard.) Roemer & Schultes
425 (A, CM, HIB, KUN, NAS, NY, PE, UC); *688* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Pennisetum alopecuroides (L.) Sprengel
1948 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Phleum alpinum L.
43 (A, CM, HIB, KUN, NA, NAS, NY, PE).
Poa nemoralis L., *s.l.**
117 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).
Setaria excurrens (Trin.) Miq.*
1111 (A, HIB, NAS, NY, PE).

CYPERACEAE

Bulbostylis densa (Wallich) Hand.-Mazz.
1969 (A, CM, HIB, KUN, NA, NAS, NY, PE, UC).

Carex brunea Thunb.
1709 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Carex gentilis Franchet*
555 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Eriophorum comosum Nees
1916 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Rhynchospora chinensis Nees & Meyen
1188 (A, CM, HIB, NAS, NY, PE).

Scirpus lushanensis Ohwi
1189 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

ARACEAE

Arisaema consanguineum Schott
87 (HIB); *788* (A, HIB).
Arisaema erubescens (Wallich) Schott*
1820 (A, HIB).
Arisaema fargesii Buchet
1604 (A, HIB).
Arisaema heterophyllum Blume*
1594 (A, HIB, NY, PE).
Arisaema lobatum Engler
1243 (A, HIB, KUN, NAS, NY, PE).

LEMNACEAE

Lemna japonica Landolt*, Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich **70:** 23. 1980.
1689 (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH).

ERIOCAULACEAE

Eriocaulon buergerianum Koern.
2061 (A, HIB, NY).
Eriocaulon robustium Makino*
1187 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

COMMELINACEAE

Streptolirion volubile Edgew.
1075 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1659* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

JUNCACEAE

Juncus effusus L.
1191 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Juncus leschenaultii Gay
1190 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1259* (A, CM, HIB, KUN, NAS, NY, PE, UC).
Juncus luzuliformis Franchet*
42 (A, HIB, NY, PE).
Juncus modicus N. E. Br.
118b (A, NA, PE, UC).
Juncus potaninii Buch.
118a (A, PE).

LILIACEAE

Aletris stenoloba Franchet
1547 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).

Allium cyaneum Regel
171 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Allium henryi C. H. Wright
870 (A, CM, HIB, KUN, NAS, NY, PE, SFDH, UC); *1713* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Allium victorialis L.
1822 (A, CM, HIB, PE).
Cardiocrinum giganteum (Wallich) Makino var. *yunnanense* (Leicht. ex Elwis) Stearn, Gard. Chron. **124:** 4. 1948.
196 (A, CM, HIB, NA, NY, UC).
Clintonia udensis Trautv. & Meyer
881 (A, CM, HIB, PE, UC).
Disporum bodinieri (Lévl. & Vaniot) Wang & Tang, Bull. Res. Peking Univ. **6:** 20. 1949, *fide* Fl. Reip. Pop. Sin. **15:** 44. 1978.
1112 (A, CM, HIB, KUN, NA, NAS, PE, UC).
Disporum cantoniense (Lour.) Merr.
733 (A, CM, HIB, KUN, NAS, PE, UC); *1160* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *1249* (A, HIB, NY, PE); *1393* (A, HIB, KUN, NA, NY, PE, UC); *1867* (A, HIB, NA, NY, PE).
Hemerocallis minor Miller
63 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1051* (A, HIB, PE).
Lilium lancifolium Thunb.
207 (A, CM, HIB, KUN, NAS, PE, UC); *361* (A, HIB; distributed as *Lilium* sp.); *685* (HIB); *855* (A, HIB, NA, NY, PE); *1059* (HIB).
Lilium taliense Franchet
1480 (A, HIB).
Liriope graminifolia (L.) Baker
454 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Ophiopogon bodinieri Lévl.
1398 (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH).
Paris polyphylla Sm.
45 (HIB); *198* (A, CM, HIB, KUN, NA, NAS, PE, UC); *304* (A, CM, E, HIB, KUN, KYO, MO, NA, NAS, NY, PE, SFDH, UC, WH); *627* (A, HIB); *886* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1396* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Polygonatum cyrtonema Hua
695 (HIB).
Polygonatum odoratum (Miller) Druce
1821 (A, HIB).
Polygonatum sibiricum Delas ex Redouté
387 (A, CM, HIB, KUN, NA, NAS, NY, PE).
Polygonatum verticillatum (L.) All.
343 (A, HIB, NA, NY); *1785* (A, CM, HIB, NAS, PE, UC).
Polygonatum zanlanscianense Pampan.
481 (A, HIB).
Reineckia carnea (Ander.) Kunth
507 (A, HIB); *1453* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

Smilacina henryi (Baker) Hara
30 (HIB).
Smilax discotis Warb.
1582 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Smilax glauco-china Warb.
477 (A, HIB, PE); *1635* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Smilax megalantha C. H. Wright*
457 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *2005* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).
Smilax menispermoidea A. DC.
731 (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC).
Smilax polycolea Warb.
632 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1223* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1340* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *1399* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Smilax riparia A. DC. var. *acuminata* (C. H. Wright) Wang & Tang, Fl. Reip. Pop. Sin. **15**: 192. 1978.
1339 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1786* (A, HIB, NY, PE).
Smilax scobinicaulis C. H. Wright
792 (A, HIB, NAS, NY, PE, UC); *1586* (A, CM, HIB, KUN, NAS, PE, SFDH, UC); *1690* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Smilax stans Maxim.
415 (A, HIB); *652* (A, HIB).
Streptopus obtusatus Fassett
48 (A, HIB, PE, UC).
Tricyrtis maculata (D. Don) Macbr.
80 (A, HIB, NA); *151* (A, CM, HIB, KUN, NA, NAS, PE, SFDH, UC); *312* (A, CM, E, HIB, KUN, KYO, NA, NAS, NY, PE, SFDH, UC, WH); *505* (A, HIB, PE, UC).
Tupistra chinensis Baker
1033 (A, HIB, NAS).
Veratrum oblongum Loes. f.
638 (HIB).

DIOSCOREACEAE

Dioscorea nipponica Makino var. *rosthornii* Prain & Burkill, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 73(Suppl. 7): 2. 1904. (syn.: *D. giraldii* R. Knuth)
233 (A, CM, HIB, KUN, NA, NAS, PE, UC); *391* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *537* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *844* (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1305* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH); *1326* (A, HIB, KUN, NA, NAS, NY, PE, UC).
Dioscorea oppositifolia L. (syn.: *D. opposita* Thunb.)
802 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC); *1470* (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Dioscorea zingiberensis C. H. Wright
1652 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).

IRIDACEAE

Belamcanda chinensis (L.) DC.
1651 (A, CM, E, HIB, KUN, NA, NAS, NY, PE, SFDH, UC, WH).
Iris wilsonii C. H. Wright
952 (A, CM, HIB, KUN, NA, NAS, NY, PE, SFDH, UC).

ZINGIBERACEAE

Zingiber mioga (Thunb.) Roscoe
2022 (A, HIB, PE).

ORCHIDACEAE

Bletilla ochracea Schlechter
476 (A, HIB, PE, UC).
Coeloglossum bracteatum (Muhl.) Parl. (syn.: *Coeloglossum viride* (L.) C. J. Hartman var. *bracteatum* (Muhl.) Richter, Pl. Europ. **1**: 278. 1890.)
885 (A, HIB, PE).
Cypripedium fasciolatum Franchet*
1808 (A, HIB).
Neottianthe cucullata (L.) Schlechter*
1796 (HIB); *1809* (A, HIB).
Neottianthe monophylla (Ames & Schlechter) Schlechter*
1185 (A, HIB, PE).
Platanthera cf. *hologlottis* Maxim.*
950 (HIB).
Pleione bulbocodioides (Franchet) Rolfe
1391 (A, HIB).

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APPENDIX 1. **Cross reference of collection numbers with collection localities,* 1980 Sino-American Botanical Expedition.**

COLLECTION NUMBERS	LOCALITY	COLLECTION NUMBERS	LOCALITY	COLLECTION NUMBERS	LOCALITY
1–25	1	*856–938*	26	*1505–1517*	43
26–50	4	*939*	27	*1518*	42
51–94	2	*940, 941*	28	*1519, 1520*	43
95–100	3	*942, 943*	27	*1521*	42
101–109	2	*944*	28	*1522–1526*	43
110–125	4	*945–966*	27	*1527–1541*	44
126–128	5	*967–976*	28	*1542–1553*	45
129–150	20	*977–998*	27	*1554, 1555*	46
151–153	3	*999–1050*	29	*1556*	47
154–178	4	*1051–1060*	8	*1557–1567*	45
179–207	5	*1061, 1062*	10	*1568–1573*	48
208–242	7	*1063–1100*	11	*1574*	50
243, 244	9	*1101–1114*	23	*1575*	49
245–250	10	*1115*	17	*1576–1591*	48
251–269	4	*1116–1118*	23	*1592–1596*	51
270–284	7	*1119*	22	*1597–1674*	52
285–298	11	*1120–1150*	24	*1675–1692*	53
299, 300	12	*1151–1181*	29	*1693–1727*	54
301–329	6	*1182*	30	*1728*	55
330–350	8	*1183*	31	*1729*	56
351–354	4	*1184–1186*	32	*1730–1735*	57
355–400	5	*1187–1275*	33	*1736*	56
401–427	11	*1276–1300*	34	*1737*	57
428–443	13	*1301–1323*	35	*1738–1770*	58
444–485	12	*1324*	36	*1771–1786*	59
486, 487	13	*1325*	35	*1787–1796*	58
488–500	14	*1326–1350*	38	*1797–1823*	60
501–532	15	*1351–1360*	34	*1824, 1825*	61
533–538	16	*1361–1363*	37	*1826–1830*	62
539	15	*1364–1378*	34	*1831–1835*	61
540–550	17	*1379–1381*	37	*1836–1849*	60
551–561	14	*1382–1384*	38	*1850*	61
562–590	17	*1385–1400*	39	*1851–1895*	63
591–599	18	*1401–1437*	40	*1896–1911*	64
600–626	19	*1438–1454*	41	*1912–1920*	65
627–650	20	*1455*	40	*1921–1924*	64
651	18	*1456–1465*	39	*1925–2000*	66
652–669	20	*1466*	42	*2001–2061*	67
670, 671	18	*1467–1472*	43	*2062–2074*	68
672	20	*1473*	42	*2075*	69
673–716	21	*1474–1484*	43	*2076–2081*	70
717–750	24	*1485*	42	*2082*	71
751–854	25	*1486–1503*	43	*2083–2085*	67
855	—†	*1504*	42		

*Collection localities are given in APPENDIX 2.

†Vicinity of Jiuhuping Forest Farm, 8 September.

APPENDIX 2. **Locality data, 1980 Sino-American Botanical Expedition.**

SHENNONGJIA FOREST DISTRICT

1.* S of Jiuhuping Forest Farm along W side of Jizigou canyon. Elev. ca. 1650 m. 25 August.
2. Ca. 0.5 km S of Jiuhuping Forest Farm in side canyon on E side of Jizigou canyon. Elev. ca. 1700 m. 25 August.
3. Side canyon on E side of Jizigou canyon directly E of Jiuhuping Forest Farm. Elev. ca. 1700 m. 25 August.
4. Vicinity of Chuifeng Pass. Elev. 2500–3000 m. 26 August.
5. Along Qiaodonggou canyon W of road between Jiuhuping Forest Farm and Bancang. Elev. ca. 1950 m. 27 August.
6. Along Yuergou canyon. Elev. 2000–2200 m. 27 August.
7. Along Miaogou canyon. Elev. 1800–1900 m. 28 August.
8. Side canyon on E side of Jizigou canyon directly E of Jiuhuping Forest Farm. Elev. ca. 1850 m. 28 August.
9. Xiaodangyang, along Dangyang River near km 53 from Xingshan Xian. Elev. ca. 1000–1050 m. 29 August.
10. Vicinity of Mucheng along Jiuchong River. Elev. ca. 1000 m. 29 August.
11. W of Hongriwan construction camp along trail leading toward Huanghunling Mt. Elev. ca. 1300 m. 30 August.
12. Laojunshan Yaowan canyon on W side of Jiuchong River, ca. 1 km S of Mucheng. Elev. 1000–1250 m. 31 August.
13. Vicinity of Mucheng along Jiuchong River. Elev. ca. 940 m. 31 August.
14. Side canyon of Mengjia River just N of bridge crossing Mengjia River N of Mucheng. Elev. ca. 1000 m. 1 September.
15. E side of Mengjia River in vicinity of Hongriwan construction camp. Elev. ca. 1300 m. 1 September.
16. Between Mucheng and Hongriwan construction camp along Mengjia River. Elev. ca. 1000 m. 1 September.
17. Along trail between Hongriwan construction camp and Qiujiaping. Elev. 1200–1400 m. 2 September (no. *1115* collected on 5 September).
18. Vicinity of Qiujiaping. Elev. ca. 1435 m. 2 September.
19. Vicinity of Qiujiaping. Elev. ca. 1440–1650 m. 3 September.
20. Along trail from Qiujiaping toward Laojun Mt. Elev. 1500–2300 m. 3 September.
21. Vicinity of Qiujiaping in side canyons on E side of Mengjia River. Elev. 1500–1900 m. 4 September.
22. Disturbed slope above Jizigou. Elev. ca. 1800 m. 4 September.
23. Ca. 1 km W of Leigutai Hydroelectric Power Station at confluence of Jiuchong and Dangyang rivers. Elev. ca. 390 m. 5 September.†
24. Vicinity of Muyuping Forest Brigade on SE side of watershed divide between Changjiang (Yangtze) and Hanjiang rivers, near km 73 from Xingshan Xian. Elev. 1450–1600 m. 7 September.
25. NE of Guanmenshan along S side of Shicao River. Elev. ca. 1150 m. 8 September.
26. Vicinity of Dalongtan and Xiaolongtan on W side of road. Elev. 2300–2600 m. 9 September.
27. Vicinity of Xiaoshennongjia. Elev. 2700–2900 m. 10 September.
28. Along road between Guanmenshan and Xiaoshennongjia. 2600–2650 m (no. *940* at 1500 m). 10 September.
29. Vicinity of Duanjiangping. Elev. 1300–1800 m. 11 September.
30. Gangou, on road between Jiuhuping Forest Farm and Dajiuhu. Elev. ca. 1700 m. 12 September.
31. Ma Mt., on road between Jiuhuping Forest Farm and Dajiuhu. Elev. ca. 1700 m. 12 September.

*Locality number.

†Localities 23 and 65 are in Xingshan Xian, just south of the Shennongjia Forest District.

32. Banbiyan, on road between Jiuhuping Forest Farm and Dajiuhu. Elev. ca. 2650 m. 12 September.
33. Zhushanyazi Pass on W side of Dajiuhu basin. Elev. 1780 m. 13 September.
34. S end of Loyang River gorge near Pingqian. Elev. ca. 1300 m. 14 September.
35. Ma Mt., on road between Jiuhuping Forest Farm and Dajiuhu. Elev. 2150 m. 14 September.
36. E side of ridge between Pingqian and Dajiuhu. Elev. 2000 m. 14 September.
37. Along road between Pingqian and Dajiuhu. Elev. 1700 m. 14 September.
38. Vicinity of Xiaojiuhu. Elev. 2000 m. 15 September.
39. Hillside above Qianjiaping. Elev. 1400–1800 m. 17 September.
40. Honghua ravine on W side of Dangyang River N of Honghua. Elev. ca. 820 m. 17 September.
41. W side of Dangyang River at km 44 from Xingshan Xian, side canyon on W-SW side of road. Elev. 725 m. 17 September.
42. Along road above Taizishang on SE side of Yingyu River canyon. Elev. 2000–2050 m. 18 September.
43. Vicinity of Taizishang along Yingyu River. Elev. 2000 m. 18 September.
44. S of Jiuhuping Forest Farm along Jizigou canyon bottom. Elev. 1900 m. 19 September.
45. Vicinity of Yinpo on road between Jiuhuping Forest Farm and Bancang. Elev. 1750 m. 19 September.
46. Between Yinpo and Qiaodonggou canyon on road between Jiuhuping Forest Farm and Bancang. Elev. 2100 m. 19 September.
47. Canyon-side on slope of SE-draining tributary of Jizigou canyon on road between Jiuhuping Forest Farm and Bancang. Elev. 2000 m. 19 September.
48. Along road between Baicaoping and Bajiaomiao. Elevation ca. 1400 m. 20 September.
49. Headquarters of Songlo Commune. Elev. ca. 1000 m. 20 September.
50. Vicinity of Xinping. Elev. 1200 m. 20 September.
51. Side canyon on E side of Songlo River directly E of Songlo Commune headquarters. Elev. 1000–1200 m. 20 September.
52. Vicinity of Houshanping on S side of Hou River. Elev. 800–1050 m. 21 September.
53. Side canyon on E side of Songlo River directly E of Songlo Commune headquarters. Elev. 1000–1200 m. 22 September.
54. Side canyon on E side of Songlo River E of Jingyin. Elev. 1050–2000 m. 22 September.
55. Just S of Tianmen Pass. Elev. 2300 m. 23 September.
56. Along road between Gumiaoya and Panshui. Elev. 1700–1850 m. 23 September.
57. Vicinity of Guijuyuan. Elev. 1800 m. 23 September.
58. Along Xigou canyon. Elev. 1700–1900 m. 24 September.
59. Vicinity of Honghe. Elev. 2050–2200 m. 24 September.
60. Along Changping River NW of Baishayuan. Elev. 1900 m. 25 September.
61. Vicinity of Shibapan. Elev. 1850 m. 25 September.
62. SE of Shibapan along Changping River. Elev. 1500 m. 25 September.
63. Vicinity of Sanyuan. Elev. 1550–1900 m (except no. *1874*: road between Baishayuan and Sanyuan. Elev. ca. 2100 m). 26 September.
64. Side canyon on S side of Dangyang River in vicinity of Sanduihe, 4 km W of Xingshan Xian line. Elev. 750 m. 29 September.
65. Canyons and cliffs along road, ca. 12 km from town of Xingshan on road between Xingshan and Jiuhuping Forest Farm. Elev. 330 m. 29 September.†

METASEQUOIA REGION OF LICHUAN XIAN

66. Metasequoia area in vicinity of Lojiaba on W side of valley. Elev. ca. 1500 m. 6 October.
67. Metasequoia area in vicinity of Zhuanjiaowan on E side of valley. Elev. ca. 1500 m. 7 October.

68. Metasequoia area in vicinity of Hongshaxi on E side of valley. Elev. ca. 1500 m. 7 October.
69. Wanjiatang, on road between city of Lichuan and Zhonglu. Elev. ca. 800 m. 8 October.
70. Metasequoia area in vicinity of Yujiawan, E of Xiaohe. Elev. ca. 1500 m. 8 October.
71. Modaoqi. 9 October.

B. B.
UNIVERSITY OF CALIFORNIA BOTANICAL GARDEN
BERKELEY, CALIFORNIA 94720
Present address:
CALIFORNIA ACADEMY OF SCIENCES
GOLDEN GATE PARK
SAN FRANCISCO, CALIFORNIA 94118

D. E. B.
CARNEGIE MUSEUM OF NATURAL HISTORY
4400 FORBES AVENUE
PITTSBURGH, PENNSYLVANIA 15213
Present address:
HARVARD UNIVERSITY HERBARIA
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

A. L. C.
KUNMING INSTITUTE OF BOTANY
ACADEMIA SINICA
KUNMING, YUNNAN

Z. C.
WUHAN INSTITUTE OF BOTANY
ACADEMIA SINICA
WUHAN, HUBEI

T. R. D.
U. S. NATIONAL ARBORETUM
WASHINGTON, D. C. 20002

S. A. H.
JIANGSU INSTITUTE OF BOTANY
HORTUS BOTANICUS NANJINGENSIS MEM. SUN YAT-SEN
NANJING, JIANGSU

Y. X. J.
WUHAN INSTITUTE OF BOTANY
ACADEMIA SINICA
WUHAN, HUBEI

Q. Y. L.
DEPARTMENT OF BIOLOGY
WUHAN UNIVERSITY
WUHAN, HUBEI

J. L. L.
THE NEW YORK BOTANICAL GARDEN
BRONX, NEW YORK 10458

S. A. S.
THE ARNOLD ARBORETUM OF HARVARD UNIVERSITY
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

S. C. S.
WUHAN INSTITUTE OF BOTANY, AND DEPARTMENT OF BIOLOGY OF WUHAN UNIVERSITY
WUHAN, HUBEI

Y. C. T.
INSTITUTE OF BOTANY
ACADEMIA SINICA
BEIJING

J. X. W.
WUHAN INSTITUTE OF BOTANY
ACADEMIA SINICA
WUHAN, HUBEI

T. S. Y.
INSTITUTE OF BOTANY
ACADEMIA SINICA
BEIJING

METASEQUOIA GLYPTOSTROBOIDES—ITS PRESENT STATUS IN CENTRAL CHINA

BRUCE BARTHOLOMEW, DAVID E. BOUFFORD, AND
STEPHEN A. SPONGBERG

DURING THE LATE SUMMER and early fall of 1980, we participated in the 1980 Sino-American Botanical Expedition to western Hubei Province in the People's Republic of China.[1] Most of our fieldwork was conducted in the Shennongjia Forest District, but a brief visit (5–10 October) was also made to the metasequoia region (lat. 30°10′N, long. 108°45′E) of Lichuan Xian (Hsien)[2] after most of the field activities were completed.

To reach the metasequoia area we traveled west by boat up the Changjiang (Yangtze) River from Yichang in Hubei Province to Wanxian in Sichuan Province (MAP 1). From Wanxian we proceeded southward by jeep back into Hubei Province to the town of Modaoqi (Mo-tao-chi), where *Metasequoia* was first discovered as a living plant. After a brief stop at the type tree of *Metasequoia glyptostroboides* Hu & Cheng (see FIGURE 1), we continued on to the town of Lichuan (the county seat of Lichuan Xian), our base of operations for the next four days. We visited the metasequoia valley (about three hours away) in Xiaohe Commune on each of three consecutive days (6–8 October). Although this region has been visited by Chinese botanists and foresters over the past four decades, we had the very great privilege to be the first foreigners to visit the area since 1948 (see below). Part of our time in the valley was spent walking or traveling to noteworthy trees of *M. glyptostroboides* and meeting with commune and local forestry officials to learn of their inventories, care, and preservation of the naturally occurring trees and their program of seed collection and propagation. We also had an interesting and informative interview with

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[1] The American participants were: Bruce Bartholomew, California Academy of Sciences (then at University of California Botanical Garden, Berkeley); David E. Boufford, Harvard University Herbaria (then at Carnegie Museum of Natural History); Theodore R. Dudley, U. S. National Arboretum; James L. Luteyn, New York Botanical Garden; and Stephen A. Spongberg, The Arnold Arboretum of Harvard University. The principal Chinese participants included: A. L. Chang, Kunming Institute of Botany; Z. Cheng, Wuhan Institute of Botany; S. A. He, Jiangsu Institute of Botany; Y. X. Jin, Wuhan Institute of Botany; Q. Y. Li, Wuhan University; S. C. Sun (expedition leader), Wuhan University and Wuhan Institute of Botany; Y. C. Tang, Institute of Botany, Beijing; J. X. Wan, Wuhan Institute of Botany; and T. S. Ying, Institute of Botany, Beijing. The expedition was conducted under the auspices of Academia Sinica and the Botanical Society of America, with funding by Academia Sinica and additional support from the National Geographic Society (Grant #2133-80) and members of the American Association of Botanical Gardens and Arboreta.

[2] The Pinyin system of romanization is used throughout except for names of older collectors, authors, and places for which changes in spelling might cause confusion. In these instances the Wade-Giles spelling is given in parentheses.

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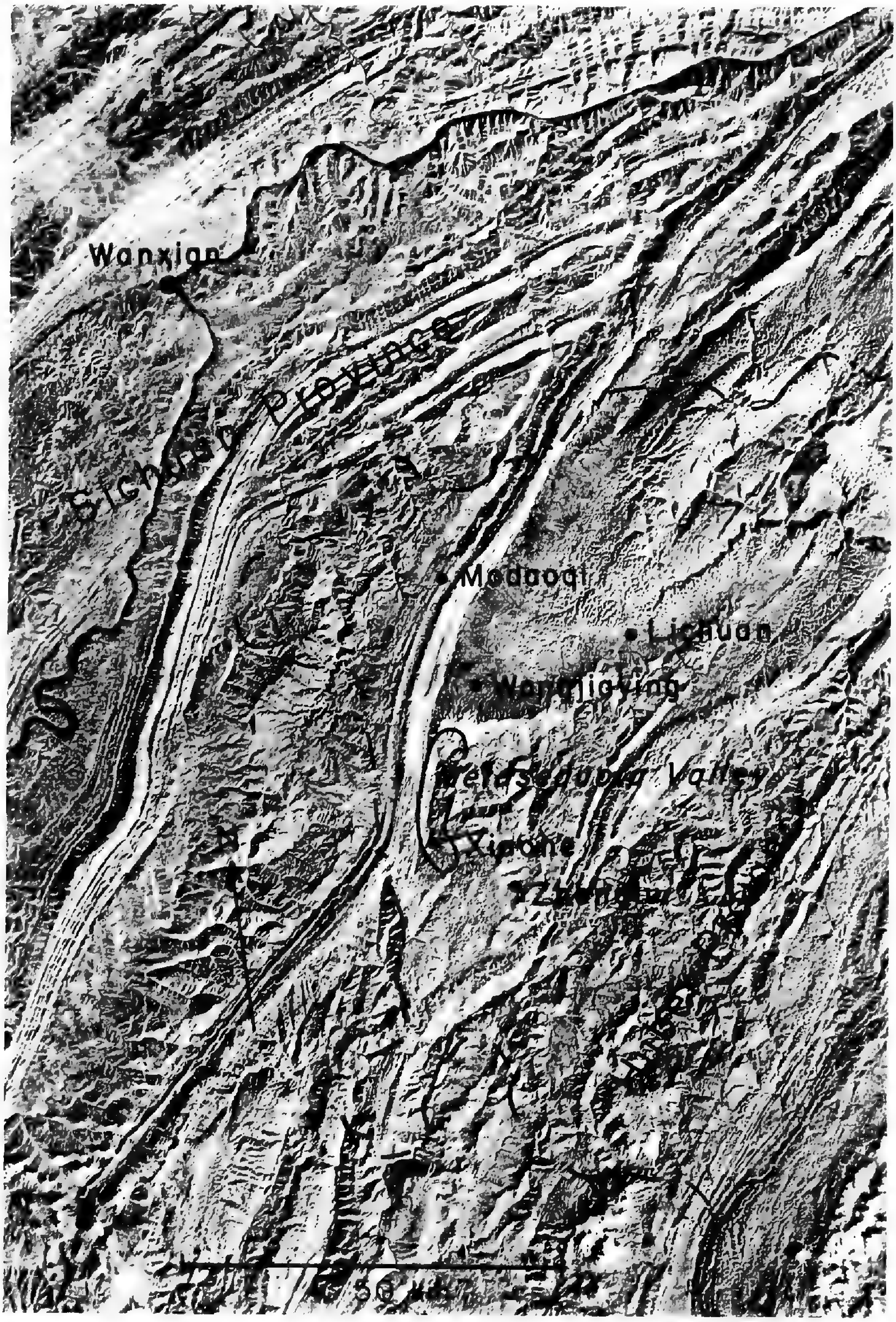

MAP 1. Metasequoia valley, Lichuan County, western Hubei Province, People's Republic of China (lat. 30°10′N, long. 108°45′E), and surrounding territory. Place names, metasequoia valley, and boundary between Hubei and Sichuan provinces superimposed on portion of NASA LANDSAT and Satellite Image (No. 8230502370500, taken 23 November 1975 and reproduced by U. S. Geological Survey EROS Data Center) to show topography of region. Wanxian located on banks of Changjiang (Yangtze) River.

two elderly members of the commune, who remembered the 1948 visit of Americans to the region. The remainder of the time was spent collecting specimens and determining the extent and nature of the vegetation associated with *Metasequoia.* No quantitative ecological data were gathered, but 161 collections of herbarium specimens were made. The identities of the vascular plants are included in the 1980 Sino-American Botanical Expedition report (Bartholomew *et al.,* 1983) and are represented by numbers *1925–2085.* Those not previously recorded for the metasequoia area are listed below.

Although we spent only a portion of three days in the valley, the limited number of firsthand reports in English concerning the natural occurrence of *Metasequoia* (Chaney, 1948; Chu & Cooper, 1950; Gressitt, 1953) makes our visit of interest. In addition, over 32 years have elapsed since the observations that served as the basis for these previous reports were made. Our impressions of current conditions in the valley are noted below.

THE DISCOVERY OF METASEQUOIA GLYPTOSTROBOIDES

The discovery of *Metasequoia glyptostroboides* as a "living fossil" has received a great deal of coverage in both the scientific and the popular literature (Fulling, 1976, 1977). However, to provide background information, we present a brief summary based on information given by Fulling (1976, 1977), Hu (1980), Böcher (1964), and Belder and Wijnands (1979) of the sequence of events surrounding the discovery and introduction of *Metasequoia* into cultivation outside of China.

Metasequoia was discovered in 1941 at Modaoqi in Sichuan Province near the border with Hubei Province[3] by T. Kan (Gan Duo), of the Department of Forestry of National Central University. Kan, however, did not collect or make specimens, and it was not until 1943 that C. Wang (Wang Zhang) of the Central Bureau of Forestry made the first collections of herbarium material. The tree was initially thought to be a form of *Glyptostrobus lineatus* (Poiret) Drude (syn.: *G. pensilis* (Staunton) Koch), but W. C. Cheng (Cheng Wanjun), of National Central University in Nanjing, realized that it represented a new genus. As a result, Cheng sent one of his assistants, C. J. Hsueh (Xue Jiru), to collect more herbarium material in February and May of 1946. In the fall of 1946, H. H. Hu (Hu Xiansu), then director of the Fan Memorial Institute of Biology, Beijing, received material from W. C. Cheng. Hu recognized that the newly discovered tree belonged to the genus *Metasequoia,* described in 1941 from Pliocene fossils by the Japanese botanist Shigeru Miki (Miki, 1941). Miki determined that certain fossils, which for nearly 100 years had been variously assigned to either *Sequoia* or *Taxodium,* actually represented a new genus, which he named *Metasequoia.* At the time, he did not realize that a living species of *Metasequoia* was still extant in south-central China.

In 1946 Cheng also sent herbarium specimens to E. D. Merrill, then director of the Arnold Arboretum of Harvard University. Merrill, realizing the significance of the new discovery, immediately arranged through Hu to obtain seeds.

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[3] After the founding of the People's Republic of China, the boundary between Sichuan and Hubei provinces in this region was changed so that Modaoqi is now in Hubei.

FIGURE 1. American participants, 1980 Sino-American Botanical Expedition to western Hubei Province, People's Republic of China, at foot of type tree of *Metasequoia glyptostroboides* just outside hamlet of Modaoqi: (from left) David E. Boufford, James L. Luteyn, Bruce Bartholomew, Stephen A. Spongberg, and Theodore R. Dudley. Chinese characters on tree trunk indicate "Lichuan County Tree Number One" and illustrate record of this tree in *Metasequoia* count.

Merrill provided $250 for Cheng to organize a collecting trip in the late summer and fall of 1947, when seeds would be mature, and Cheng assigned C. T. Hwa (Hua Jingan) to undertake the expedition. During the three-month collecting period, Hwa found trees of *Metasequoia* scattered over an area of about 800 km^2, with the largest concentration (what he thought to be about 1000 trees) in the Shuishaba (Shui-sa-pa) valley of western Hubei.[4] About 1 kg of mature seeds was collected on this expedition, and Cheng sent the initial batch to the Arnold Arboretum in December, 1947. It has generally been thought that this was the first introduction of living *Metasequoia* into the West. However, based on evidence provided by Böcher (1964, in legend to *fig. 1*) and Belder and Wijnands (1979), Cheng apparently also sent seeds to Copenhagen and Amsterdam at the same time that he sent them to Merrill at the Arnold Arboretum; thus, the introduction of *Metasequoia* into the West was essentially simultaneous in Europe and North America. (This information differs from that given by Fulling (1976)). Merrill immediately distributed seeds to institutions and interested individuals around the world, and one recipient was Ralph W. Chaney, a paleontologist at the University of California, Berkeley.

Early in 1948 Chaney traveled to see *Metasequoia* in the wild. He was accompanied by Milton Silverman, who was then science writer for the *San Francisco Chronicle.* Chaney and Silverman were in the metasequoia area for five days in March, 1948, and returned with seeds and several seedlings of *Metasequoia.*

Fulling (1976) believed that Chaney did not collect seeds of *Metasequoia,* but according to Silverman (pers. comm.), he and Chaney collected seeds from cones on the ground. Chaney and Silverman divided these seeds in China (Silverman returned to the United States first), and they each carried some back. The fact that Chaney brought seeds back is corroborated by Jean Spitzer, a stewardess on the Pan American flight that Chaney took from Wake Island to Honolulu. According to Mrs. Spitzer (pers. comm.), Chaney told her of the seeds, which he had in an inside pocket of his coat, and stated that he was not going to declare them at Honolulu—he feared that the seedlings of *Metasequoia* he had with him might be confiscated and did not want to lose the seeds as well.

Later in 1948 two additional expeditions, one led by Cheng and the other by J. L. Gressitt, of Lingnan University, stayed for extended periods in the metasequoia area. Gressitt was mainly interested in collecting insects associated with *Metasequoia,* but he also made plant collections that, in addition to seeds and herbarium specimens from the Cheng expedition, were sent to the Arnold Arboretum. The herbarium material from these two expeditions served in large part as the basis for Hu's floristic analysis (1980). Gressitt also collected seeds and seedlings of *Metasequoia,* and these were sent to Lingnan University and to the California Academy of Sciences in San Francisco (Gressitt, pers. comm.).

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[4] The valley containing the main *Metasequoia* population is usually referred to in the literature as Shuishaba (Shui-sa-pa); however, according to Xi Xingwen, head of the Xiaohe Commune, the name Shuishaba only refers to the region immediately around the hamlet of Shuishaba rather than to the entire valley.

THE TYPE TREE OF METASEQUOIA GLYPTOSTROBOIDES

The original tree from which the type specimens of *Metasequoia glyptostroboides* were taken is still growing just outside of Modaoqi, about 35 km north of Xiaohe, where the main *Metasequoia* population occurs. Gressitt (1953) reported that two smaller trees of *Metasequoia* occurred in a row with the type tree, but in 1980 only the one large tree remained at this location. Inquiries in Modaoqi about the other two drew a complete blank. There are now many *Metasequoia* trees along the road that passes through Modaoqi, but these have been planted during the past 30 years, along with *Cryptomeria japonica* (L. f.) D. Don, as the principal roadside trees in the area.

In 1948 there was a small shrine on one side of the type tree and a shed on the other. Both of these structures have been removed. The tree looks essentially the same now as it does in photographs taken in 1948 (see FIGURES 2, 3). It appears to be in excellent health and was bearing seed-filled cones in October, 1980. However, it has grown only very slightly over the past 30 years. We measured the buttress reported as 230 cm in diameter in the late 1940's (Hu & Cheng, 1948): it was 241 cm across, and the diameter of the trunk above the buttress was 167 cm. Based on partial cores, Chaney estimated this tree to be 300 years old (Chu & Cooper, 1950). Extrapolations from partial cores made in 1977 yielded an estimated age of 450 years.

PRESENT STATUS OF NATURALLY OCCURRING METASEQUOIA

Almost all of the naturally occurring trees of *Metasequoia* grow in the central valley of Xiaohe Commune. Since 1974 the Bureau of Forestry of Lichuan Xian has maintained a staff of five people in the Commune, with one of their objectives being to measure each tree every four years. The Forest Bureau has counted and numbered 5420 trees with a d.b.h. of at least 20 cm. We were told that approximately 1700 to 1800 of these are mature, seed-producing trees. The tallest recorded trees in the valley are on the east side in the vicinity of Hongshaxi: several reach a height of about 50 m, but they have smaller trunk diameters than the one that grew at Wangjiaying (see below). The oldest tree in Xiaohe Commune (approximately 420 years, estimated from a partial coring made in 1977) is near the town of Xiaohe (FIGURE 4); in 1980 it had a d.b.h. of 160 cm.

There are several outlying populations and individuals (Ling, 1976; Liu *et al.*, 1978; Zhang Fengyun, pers. comm.) in addition to the major *Metasequoia* population at Xiaohe. Near the town of Zhonglu (ca. 15 km southeast of Xiaohe), there are about ten trees, with a d.b.h. of 40–50 cm; in Shizhu Xian (about 40 km west of Xiaohe in Sichuan Province) there are two; in Longshan (in northwestern Hunan Province about 110 km southeast of Xiaohe), three (two growing together and one some distance away). Another outlying tree is the type tree at Modaoqi.

There was previously an isolated tree at Wangjiaying, discovered by Hwa in 1947 (Hu & Cheng, 1948); with a diameter of 2.2 m and a height of about 50 m, it was the largest recorded *Metasequoia* (Chu & Cooper, 1950). This tree

FIGURES 2, 3. Type tree of *Metasequoia glyptostroboides.* 2, photograph taken in 1948 by J. L. Gressitt. Note shrine at base of tree. 3, photograph taken on 5 October 1980. Shrine removed, and tree now surrounded by rice paddies and small, ditched stream. Buildings in background constructed since 1948.

was also seen by Gressitt in 1948 (Gressitt, 1953). Unfortunately, lightning struck it in 1951, splitting it into three parts and killing it. Another large tree, with a diameter of 2 m, was found between the main population in Xiaohe Commune and the three trees in Hunan Province, but it was cut down during the Cultural Revolution.

In its natural habitat *Metasequoia* is now protected by the government, and not even small trees may be cut. The trees that we saw (including the two ancient ones at Modaoqi and Xiaohe) all appeared to be in good health. However, we did not see any small seedlings. This differs from the situation in 1948, when Chu and Cooper (1950) found seedlings in thickets surrounding older *Metasequoia* trees. In 1980 vegetation was either absent around the trees of *Metasequoia,* or very closely cropped (see FIGURE 5), presumably by the local people and not by animals. The lack of governmental protection of the habitat (and thus the lack of associated vegetation) probably accounts for the lack of seedling establishment.

THE "METASEQUOIA FLORA"

The occurrence of *Metasequoia* trees in the main valley is essentially the same as that reported by Chu and Cooper (1950) and Gressitt (1953): *Metase-*

FIGURE 4. Oldest *Metasequoia* tree in Xiaohe Commune (approximately 420 years old, based on partial corings made in 1977, and with d.b.h. of 160 cm in 1980).

quoia grows primarily along the sides of the valley, and most of the flat land in the valley is planted in rice.

There have been a number of reports of plants associated with *Metasequoia*

(Chaney, 1948; Chu & Cooper, 1950; Hu, 1980). It is of interest to compare these reports with the present situation of *Metasequoia* in Xiaohe Commune. Chaney (1948) enumerated a few species and genera that he recognized, but his report was fragmentary and not based on the collection of specimens. In contrast, the paper by Hu (1980) was based on all of the material in the Arnold Arboretum herbarium that was collected in the metasequoia area in the late 1940's. It enumerates 550 species of vascular plants belonging to 301 genera and 127 families. Based on our firsthand observations, it is our impression that Hu's paper gives a very deceptive picture of the plants associated with *Metasequoia*, and that it is not accurate to refer to these 550 species as the "*Metasequoia* Flora." Although most of the specimens seen by Hu were collected in the vicinity of the metasequoia valley, it is quite likely that many were collected at higher elevations than where *Metasequoia* grows, and some were, no doubt, from cultivated trees. Hu admits the cultivated status of *Ginkgo biloba* L., and it is probably also true for such others as *Pinus armandii* Franchet (Gressitt, 1953, p. 49, reported one large tree in Shuishaba (*Gressitt 2536*) but many more near Modaoqi), *Juniperus formosana* Hayata (Gressitt, 1953, p. 51, reported two trees at "Suen-wu" and another on the approach to "Suen-wu"), and *Keteleeria davidiana* (Bertrand) Beissner (we saw two very large trees of this near a school a short distance from Xiaohe). It is also clear from the accounts of Gressitt's treks in search of other populations of *Metasequoia* that many of the plants he collected were found at some distance from the known *Metasequoia* stands, and many were from high elevations or from habitats unsuitable for *Metasequoia* (Gressitt, 1953). Also, of the 18 species of gymnosperms listed by Hu (1980) for the "*Metasequoia* Flora," we saw only one, *Cunninghamia lanceolata* Hooker, outside of cultivation and in close proximity to *Metasequoia*. However, *Cunninghamia* is restricted to drier habitats on well-drained slopes above *Metasequoia*. Chu (Chu & Cooper, 1950) also found *Taxus chinensis* Rehder in his quadrats and reported *Cephalotaxus fortunei* Hooker as being nearby. Chu and Cooper (1950, p. 272) noted that of the 33 tree species growing either in the *Metasequoia* quadrats or nearby, "only four are gymnosperms." Similar examples of cultivated angiosperms growing with *Metasequoia* can likely be found. Hu herself (1980, p. 49) considers that at least 13 listed angiosperms do not grow in the metasequoia community.

Chu and Cooper's study (1950), derived from Chu's quadrat analysis, is the only report on plants associated with *Metasequoia* based on systematic studies. Chu's quadrats were placed in areas that included *Metasequoia* and were made during the 1948 expedition to the metasequoia area led by W. C. Cheng. Specimens from this expedition labeled as collected by *W. C. Cheng–H. T. Hwa* were part of the material used by Hu (1980). However, although Chu and Cooper (1950, p. 273) stated that "nearly one hundred species of herbs, including the lower forms, have been collected from the area in which *Metasequoia* grows," they did not indicate that vouchers for the quadrat studies had been made. There are plants reported by Chu (see below) that were not represented among the specimens available to Hu. If there were vouchers made for Chu's quadrat studies, they were not among the material sent to the Arnold Arboretum. It is also unfortunate that not all of Chu and Cooper's determinations are

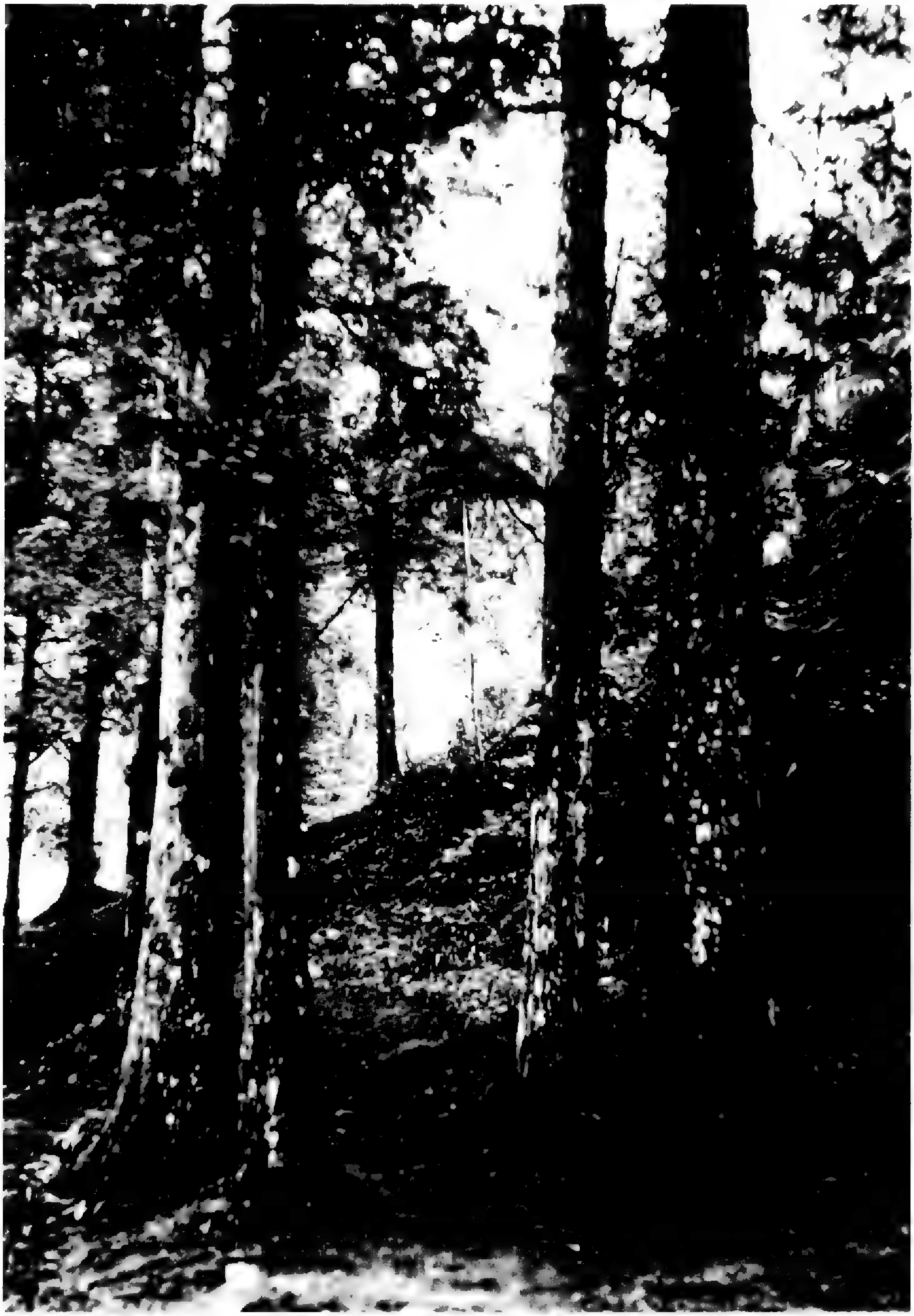

FIGURE 5. Grove of *Metasequoia glyptostroboides* growing at bottom of small ravine above main valley floor near village of Xiaohe. Note absence of associated plants.

complete. In light of the deterioration of the vegetation in the metasequoia valley, and especially that growing in close association with *Metasequoia,* if vouchers for this study are extant in some herbarium in China, a reworking of the determinations of the material would give the best picture of the plants originally associated with *Metasequoia* that will ever be possible.

The habitat of *Metasequoia* is reminiscent of that of *Taxodium distichum* (L.) Rich. in the southeastern United States, a parallel previously drawn by Chaney (1948). *Metasequoia* is a riparian species, and before habitation the valley floor may well have been a *Metasequoia* forest (see below). *Metasequoia* trees that occur away from the valley floor are restricted to the moist bottoms of ravines and draws that drain into the main valley (see FIGURE 5). *Taxodium* commonly occurs in flat, poorly drained depressions behind natural levees along slow-moving rivers. Based on this similarity of habitats, on reports of the species associated with *Metasequoia* (Chaney, 1948; Chu & Cooper, 1950; Gressitt, 1953), on Hu's (1980) enumeration of the "*Metasequoia* Flora," and on our own observations both in the southeastern United States and in the metasequoia valley in 1980, it is possible to hypothesize a past *Metasequoia* forest analogous to present-day *Taxodium distichum* forests. Among the dominant tree species usually found with *Taxodium distichum* are *Nyssa aquatica* L., *N. sylvatica* var. *biflora* (Walter) Sarg., *Populus heterophylla* L., *Quercus* spp., *Liquidambar styraciflua* L., *Carpinus caroliniana* Walter, *Betula nigra* L., *Acer rubrum* L., *Ulmus americana* L., *Carya* spp., *Fraxinus* spp., and *Salix* spp. The associated shrubs include *Ilex* spp., *Viburnum* spp., *Itea virginica* L., *Cornus* spp., and *Lindera benzoin* (L.) Blume. The vines include *Berchemia scandens* (Hill) K. Koch, *Bignonia capreolata* L., *Rhus radicans* L., *Decumaria barbara* L., *Parthenocissus quinquefolia* (L.) Planchon, *Vitis* spp., *Ampelopsis* spp., and *Smilax* spp. While each of the species of this group has specific microhabitat requirements, all are usually found growing in close proximity to *Taxodium.*

In their list of plants growing with *Metasequoia,* Chu and Cooper (1950) included species of many of the same genera. We noted several large trees of *Liquidambar acalycina* (*L. formosana* Hance *in* Chu & Cooper, 1950; and *in* Hu, 1980) and species of *Salix, Acer, Pterocarya,* and *Quercus* in habitats similar to those occupied by *Metasequoia,* but not on the adjacent slopes. Moreover, it seems likely that at one time the floor of the metasequoia valley was occupied by trees that were tolerant of periodic flooding, could grow in poorly drained soils, and occupied more or less specific microhabitats. Among the species listed as being associated with *Metasequoia glyptostroboides* by Chu and Cooper (1950), Gressitt (1953), and Hu (1980), the following grow in habitats similar to those of their American counterparts associated with *Taxodium*: *Houttuynia cordata* Thunb. (in place of *Saururus cernuus* L. in the southeastern United States); *Populus adenopoda* Maxim.; *Salix* spp.; *Pterocarya hupehensis* Skan, *P. paliurus* Batalin, and *P. stenoptera* C. DC. (all in place of *Carya* spp.); *Betula luminifera* Winkler; *Carpinus fargesii* Franchet; *Quercus* spp.; *Morus* sp.; *Cocculus orbiculatus* (L.) A. P. DC.; *Ulmus multinervis* Cheng; *Lindera glauca*; *Liquidambar acalycina* Chang; *Ilex* spp.; *Berchemia* spp.; *Nyssa sinensis* Oliver; *Cornus controversa* Hemsley and *C. macrophylla* Wallich; *Clethra fargesii* Franchet; *Styrax bodinieri* Lévl. and *S. suberifolius* Hooker f. & Arnott (*S. japonica* Sieb. & Zucc. was reported by Chu and Cooper

(1950) as being in the quadrats but is not included in Hu's (1980) enumeration); *Viburnum* spp.; and *Smilax* spp.

These similarities, however, should not be taken as evidence that the associations we see now have existed over long periods of time. Hu (1980, p. 64) states that "the vegetation of the metasequoia area is a living sample of a comparatively well-preserved ancient flora." It is highly doubtful that this is true. It would perhaps be better to say that the flora in the metasequoia region contains a number of genera that have fossil records dating back to the Tertiary and ecological adaptations enabling them to grow together at present. Davis (1976) has compiled data showing that the forests of eastern North America and Europe, which are often thought of as stable communities, are actually the result of differential migrations in the past of the individual components that have come together only fairly recently. She has shown that the current associations may be a feature of the present, and that the species growing together now often occurred in different associations and abundance even within the past few thousand years. The fact that we see members of genera with long geologic histories growing together today in the metasequoia region of China only indicates that their ecological tolerances overlap; it gives no indication that their migrational or evolutionary histories have coincided.

Davis (1976) suggests that the glacial periods (perhaps as many as 16 in North America and Europe), each of which lasted 50,000–100,000 years, are the normal and most stable phases of the Pleistocene, while the interglacials, which lasted only 10,000–20,000 years each, were catastrophic periods. There is little reason to believe that the climate of eastern Asia remained unchanged during this time when the climates in North America and Europe were undergoing such wide fluctuations. It seems almost certain that there would have been widespread migrations in the Asian flora like there were in North America and Europe, and that what we see now are the assemblages of species (communities) resulting from the sorting out of the flora in response to the rather drastic changes in climate during the glacial and interglacial periods of the Pleistocene and Holocene.

Chu and Cooper (1950) stated that *Metasequoia* appears to grow naturally only in sandy soil derived from Jurassic sandstone, and that only cultivated trees grow over limestone. They also mentioned that the valley floor is derived mainly from sandstone, providing rather strong suggestive evidence that the floor could have been occupied—and perhaps dominated—by much more extensive stands of *Metasequoia.* Additional evidence of a once more-widespread *Metasequoia* forest on the valley floor is provided by several large trunks of *Metasequoia* that we saw that had recently been unearthed in the center of paddy fields far from the nearest slopes and ravines where the trees now grow. Altogether, more than 200 of these trunks, many over two meters in diameter, have been found in the paddies along the level floodplain of the main river and side streams (T. S. Ying, pers. comm.). Also (according to Liu *et al.,* 1978), some of the houses in the valley were constructed of boards cut from *Metasequoia.* These houses are believed to be 200–300 years old and date roughly from the time of the original settlers.

FIGURES 6, 7. General views of metasequoia valley. 6, photograph taken in 1948 by J. L. Gressitt. Note forest-covered slopes in background, and fields only on level valley floor. 7, photograph taken in 1980. Note extensive cultivation of rice on valley floor and on terraced fields on lower slopes. Columnar trees along edges of paddies an admixture of *Metasequoia glyptostroboides* and *Cunninghamia lanceolata,* with columnar habit due to pruning of lateral branches for firewood.

CLIMATE

There are no climatic data available for Xiaohe Commune. The nearest weather station is in Lichuan, 40 km northeast of Xiaohe, but data from this station[5] give a much more accurate picture of the climate where *Metasequoia* grows than do those reported by Chaney (1948), which were based on information obtained from Zhongjing (Chungking), or those used by Chu and Cooper (1950) based on records from Guiyang (Kweiyang). Lichuan is at an elevation of about 1070 m (essentially the same as the floor of the metasequoia valley) and is within the range of *Metasequoia,* if one includes the outlying populations and individuals.

TABLE 1 presents temperature records from Lichuan for the years 1959–1978. The lowest monthly mean minimum temperature is −6.1°C for January, and the absolute lowest temperature is −15.4°C recorded in February, 1972. These temperatures are nowhere near the physiological lower limit of *Metasequoia* since trees survive the winters in Jamaica Plain, Massachusetts, where temperatures as low as −23°C have been recorded. The highest monthly mean maximum in Lichuan is 32.2°C for August, and the absolute highest temperature is 35.4°C recorded in August, 1959. This is also not the physiological upper limit for *Metasequoia.* In St. Louis, Missouri, where *Metasequoia* is used as an ornamental and street tree, temperatures higher than 38°C are not uncommon.

Precipitation data for Lichuan are given in TABLE 2. Rainfall is very seasonal: two thirds of the total amount occurs in the five-month period from May through September, and less than one sixth from November through March. There were no months lacking rain between 1959 and 1978, although only a trace (1.1 mm) was recorded in January, 1963. During this 20-year period the wettest year was 1975, with 1529 mm of rain; the driest was 1966, with 863.1 mm.

Without data from Xiaohe Commune, it is impossible to compare the climate there with that of Lichuan, but the fact that the valley is completely enclosed would probably provide for some insulation and moderation of the climate. Of particular note is the ridge about 1500 m in elevation that bounds the valley to the north. One might expect that the absolute minimum temperature in the metasequoia valley would be somewhat higher than in Lichuan.

THE HUMAN POPULATION IN THE METASEQUOIA VALLEY

The Lu family, the first to settle in the metasequoia valley, moved into the area about 310 years ago.[6] They settled in the area now occupied by the hamlet of Jiantianba, about 7 km west of the present town of Xiaohe. Xiaohe itself

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[5] Weather records from the Lichuan Weather Station were supplied by Zhang Fengyun, director of the Lichuan Forest Research Institute.

[6] Information on Xiaohe Commune was supplied by Xi Xingwen, head of Xiaohe Commune.

TABLE 1. **Temperature records (°C) for Lichuan, Hubei Province, People's Republic of China, 1959-1978.**

	MONTH											
RECORD	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Monthly mean	1.7	3.0	7.8	12.9	16.9	20.3	23.3	22.8	18.6	13.6	8.1	3.6
Monthly mean maximum	12.5	15.6	21.5	26.5	27.8	30.7	32.2	32.3	29.3	24.5	18.6	14.5
Monthly mean minimum	−6.1	−5.8	−1.6	2.7	8.7	11.9	15.8	14.7	9.3	3.9	−1.2	−3.7
Absolute maximum	16.9	20.0	27.1	30.2	30.6	32.9	34.8	35.4	32.0	27.5	22.1	17.7
Absolute minimum	−13.8	−15.4	−3.5	−1.5	5.9	8.6	13.7	12.2	7.1	−0.6	−3.5	−8.2

TABLE 2. **Precipitation records (mm) for Lichuan, Hubei Province, People's Republic of China, 1959-1978.**

	MONTH												
RECORD	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	ANNUAL TOTAL
Mean monthly precipitation	18.7	30.0	67.9	109.5	187.5	183.8	171.9	144.1	170.8	109.2	61.2	28.3	1282.9
Percentage of annual total	1.5	2.4	5.3	8.5	14.6	14.3	13.4	11.2	13.3	8.5	4.8	2.2	100
Lowest monthly precipitation	1.1	6.0	26.6	60.2	74.9	55.7	15.9	24.6	47.0	19.3	26.6	8.7	
Highest monthly precipitation	40.7	71.1	117.3	179.7	321.1	383.2	293.9	307.6	378.9	204.0	121.9	55.6	

was first settled by the Wu family about 200 years ago. Chu and Cooper (1953), however, reported that the Wu family was the first family to settle in the valley. The family names Lu and Wu are still common in the area.

It seems probable that the flat valley floor with its *Metasequoia* stands was the first site to be cleared for agriculture when the original inhabitants settled the valley (FIGURES 6, 7). The settlers most likely cleared vegetation from the richest and easiest areas for cultivation but left the trees in marginal areas such as immediately along the river or in the narrow ravines leading into the main valley. Perhaps some trees were also spared due to their large size or because of possible religious significance.

The valley containing the main *Metasequoia* population is in Xiaohe Commune. This commune occupies a total area of 10,640 ha and has a population of 21,000 people, of whom 12,000 live in the valley itself, mostly in scattered hamlets of several houses situated along the edges of the valley. Within the valley there are 670 ha of rice paddies and 1400 ha of other fields; outside there are an additional 1270 ha of nonpaddy fields planted in corn and other crops. In addition to the fields, the commune contains 7300 ha of mountainous land.

The high population density in Xiaohe Commune (if the figures we were given are correct, there are 6.287 persons per ha or only 0.159 ha per person!) has resulted in considerable damage to the local vegetation. Both Chu and Cooper (1950) and Gressitt (1953) reported that the forests had largely been destroyed by the time of their visits, and even the *Metasequoia* communities showed signs of alteration due to man's activities. We found that conditions had deteriorated even more since these reports. Our observations indicate that there has been so much human and domestic animal disturbance that there are very few plants now associated with *Metasequoia* (FIGURE 5). However, there are areas in Xiaohe Commune, particularly in side ravines and on slopes on the east side of the main valley, where secondary forests are developing. Although these areas are close to the *Metasequoia* groves, they are separated from the riparian areas occupied by *Metasequoia* by cut-over slopes and cultivated fields. Comparison of the present condition of the forests with pictures taken in 1948 shows considerable destruction during the past 32 years (see FIGURES 6–9). We were told that many large trees, particularly *Castanea henryi* Rehder & Wilson and *C. mollissima* Blume, were cut in the mid to late 1950's during the Great Leap Forward to make charcoal for smelting iron. However, no significant amount of iron was ever produced.

The protected status currently given by the government to the remaining naturally occurring trees of *Metasequoia* will probably insure their survival for the immediate future, but the lack of protection for the surrounding habitat will likely result in little, if any, natural reproduction. The thickets that Chu and Cooper (1950) mentioned as being around many of the trees are no longer there, and it was in those habitats that they reported finding seedlings and small trees of *Metasequoia*. The efforts to monitor the natural populations of *Metasequoia* may have resulted in disturbance and clearing of other vegetation, thereby contributing to the destruction of suitable germination sites.

FIGURE 8. Small side valley connecting with eastern portion of metasequoia valley (photograph taken by J. L. Gressitt in 1948). Note relatively undisturbed forest surrounding terraced field.

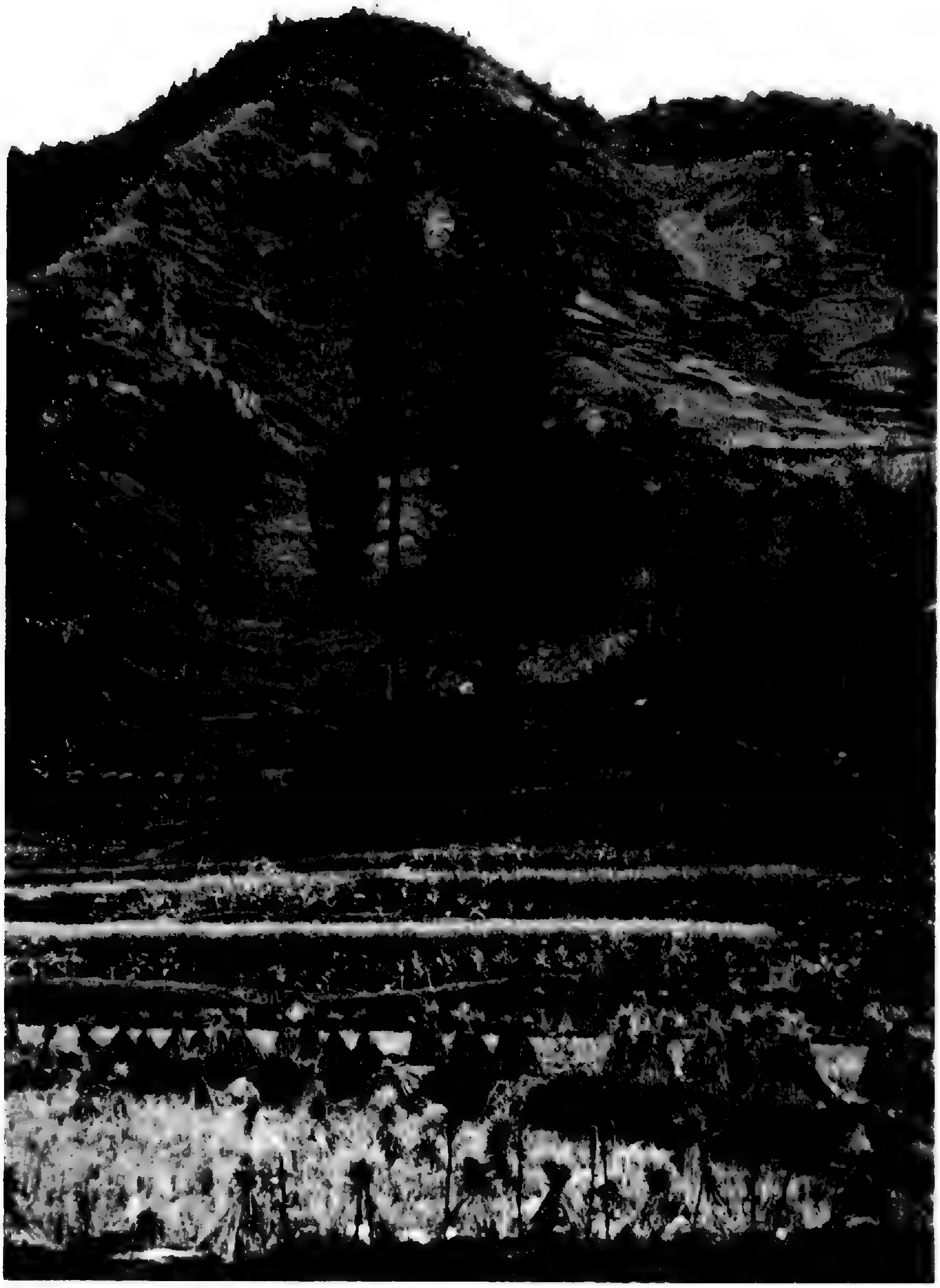

FIGURE 9. Highly disturbed slopes of side valley showing results of human habitation (photograph taken in 1980). Upper slopes largely denuded of native vegetation and lower slopes given over to rice paddies and corn fields. Tree behind building is *Ginkgo biloba*.

ACKNOWLEDGMENTS

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We would like to express our particular thanks to J. Linsley Gressitt, who kindly reviewed the manuscript and made available for our use photographs he had taken in the metasequoia valley in 1948. It was with great sadness that we learned of Gressitt's and his wife's deaths in an airplane crash in China on April 26, 1982, when Gressitt was on his first return visit to the People's Republic since the early 1950's. As a tribute to his pioneering work in the metasequoia area, we dedicate this paper to his memory.

ADDITIONS TO THE FLORA OF THE METASEQUOIA REGION

Of the 160 numbers collected in the metasequoia valley on the 1980 Sino-American Botanical Expedition, 122 of them represent taxa of vascular plants. Of these, 71 have not been previously reported from the valley. The following enumeration presents these additions to the flora of the region. Collection numbers of the Sino-American Botanical Expedition are in parentheses. The 20 taxa reported as associated with *Metasequoia* by Chu and Cooper (1950) that are not in Hu's (1980) enumeration are also included here; these names are followed by an asterisk. The arrangement of taxa follows the same scheme used in the report of the 1980 Sino-American Botanical Expedition to western Hubei (Bartholomew *et al.,* 1983), and reference to that paper is suggested for annotations and discussions of taxonomic problems and for descriptions of new taxa.

PTERIDOPHYTA

LYCOPODIACEAE

Lycopodium crispatum Ching (*1974*)

HYMENOPHYLLACEAE

Hymenophyllum barbatum Bosch (*2023*)

DENNSTAEDTIACEAE

Microlepia marginata (Houtt.) C. Chr. (*2052*)

HYPOLEPIDACEAE

Hypolepis punctata (Thunb.) Mett. (*1943, 1944*)

PTERIDACEAE

Pteris wallichiana Agardh (*2026*)

HEMIONITIDACEAE

Coniogramme robusta Christ var. *repandula* Ching (*2049*)

WOODSIACEAE

Peranema cyathioides D. Don (*2085*)

BLECHNACEAE

Woodwardia unigemmata (Makino) Nakai (*2057*)

ATHYRIACEAE

Athyrium epirachis (Christ) Ching (*2011*)
Athyrium vidallii (Franchet & Sav.) Nakai (*2053*)
Lunathyrium vermiforme Ching, Boufford, & Shing (*2025*)
Lunathyrium wilsonii (Christ) Ching (*2048*)
Pseudocyclosorus tsoi Ching (*1946*)

DRYOPTERIDACEAE

Dryopteris labordei (Christ) C. Chr. (*2054*)
Dryopteris supraimpressa Ching, Boufford, & Shing (*2020*)
Polystichum lobatopinnulum Ching, Boufford, & Shing (*2059*)

ASPLENIACEAE

Asplenium tripteropus Nakai (*2046*)

POLYPODIACEAE

Arthromeris cuneata Ching (*1971, 2029*)
Drymotaenium miyoshianum (Makino) Makino (*2058*)
Lepidogrammitis drymoglossoides (Baker) Ching (*2027*)
Lepidomicrosorium subhastatum (Baker) Ching (*2083*)

AZOLLACEAE

Azolla imbricata (Roxb.) Nakai (*2056*)

ANGIOSPERMAE

DICOTYLEDONES

FAGACEAE

Castanea seguinii Dode*
Quercus glandulifera Blume (*1931*)

MORACEAE

Ficus foveolata Wallich*
Morus alba L.*

URTICACEAE

Gonostegia hirta (Blume) Miq. (*1937*)

POLYGONACEAE

Polygonum caespitosum Blume (*1956*)
Polygonum hydropiper L. (*1954*)
Polygonum muricatum Meisner (syn.: *P. strigosum* R. Br. var. *muricatum* (Meisner) A. N. Steward) (*1955*)
Polygonum persicaria L. (*2015*)
Polygonum thunbergii Sieb. & Zucc. (*1953*)

RANUNCULACEAE

Clematis urophylla Franchet (*1940*)

LARDIZABALACEAE

Akebia trifoliata (Thunb.) Koidz.*
Holboellia sp.*

BERBERIDACEAE

Berberis sargentiana Schneider (*1938*)
Berberis virgetorum Schneider (*2079*)

SCHISANDRACEAE

Schisandra pubescens Hemsley & Wilson*

LAURACEAE

Phoebe neurantha (Hemsley) Gamble (*2045*)

HAMAMELIDACEAE

Corylopsis veitchiana Bean (*2033*)
Liquidambar acalycina Chang (*1950*)

ROSACEAE

Cotoneaster aff. *dielsiana* Pritzel (*1935*)
Pyracantha crenulata (D. Don) Roemer (*1961*)
Pyracantha fortuneana (Maxim.) H. L. Li*
Rosa henryi Boulenger*
Rubus amphidasys Focke ex Diels (*2076*)
Rubus lambertianus Sér. (*1936*)
Rubus setchuenensis Bur. & Franchet (*1952*)

LEGUMINOSAE

Dalbergia stenophylla Prain*

SIMAROUBACEAE

Picrasma quassioides Benn.*

RUTACEAE

Euodia rutacarpa (Juss.) Bentham var. *bodinieri* (Dode) Huang (*1947*)

EUPHORBIACEAE

Acalypha australis L. (*1973*)
Mallotus tenuifolius Pax* (author as Muell.-Arg. *in* Chu & Cooper, 1950)

BUXACEAE

Sarcococca humilis Stapf (syn.: *S. hookeriana* Baillon var. *humilis* Rehder & Wilson) (*1967*)

RHAMNACEAE

Rhamnus davuricus Pallas (*2024*)

CELASTRACEAE

Euonymus kiatschovicus Loes. (*2075*)
Microtropis triflora Merr. & Freeman (*2018*)

VITACEAE

Parthenocissus tricuspidata (Sieb. & Zucc.) Planchon*
Tetrastigma hemsleyanum Diels & Gilg (*2010*)

SABIACEAE

Meliosma dilleniifolia (Wallich ex Wight & Arnott) subsp. *flexuosa* (Pampan.) Beus. (*1949*)
Meliosma oldhamii Miq.* (syn.: *M. pinnata* (Roxb.) Maxim. subsp. *barbulata* Cufod. var. *oldhamii* (Maxim.) Beus.)

BALSAMINACEAE

Impatiens cf. *exiguiflora* Hooker f. (*1960*)

THEACEAE

Eurya loquaiana Dunn (*2028*)
Eurya obtusifolia Chang (*2004*)

LYTHRACEAE

Rotala indica (Willd.) Koehne (*2084*)

ARALIACEAE

Nothopanax davidii (Franchet) Harms ex Diels*

CORNACEAE

Cornus kousa Hance var. *angustata* Chun (*2032*)

ERICACEAE

Rhododendron fortunei Lindley subsp. *discolor* (Franchet) Chamberlain (*2040*)

MYRSINACEAE

Ardisia crispa (Thunb.) DC.*
Ardisia japonica (Thunb.) Blume (*1926*)

OLEACEAE

Jasminum urophyllum Hemsley (*2078*)

GENTIANACEAE

Tripterospermum affine (Wallich) H. Sm. (*1927*)

LABIATAE

Clinopodium polycephalum (Vaniot) C. Y. Wu & Hsuan (*1968*)
Elsholtzia ciliata (Thunb.) Hylander (*1962*)
Elsholtzia flava Bentham (*1945*)
Mosla scabra (Thunb.) C. Y. Wu & H. W. Li (*1965*)

SCROPHULARIACEAE

Veronicastrum caulopterum (Hance) Yamazaki (*2008*)

RUBIACEAE

Anotis hirsuta (L. f.) Boerl. (*2006*)

CAPRIFOLIACEAE

Lonicera japonica Thunb.*
Lonicera pileata Oliver*
Lonicera similis Hemsley*
Viburnum cylindricum Buch.-Ham. ex D. Don (*1930*)
Viburnum foetidum Wallich (*2002*)

COMPOSITAE

Ainsliaea gracilis Franchet (*1970, 2041*)
Lactuca graciliflora (Wallich) DC. (*2017*)
Solidago decurrens Lour. (*2016*)

MONOCOTYLEDONES

GRAMINEAE

Isachne nipponensis Ohwi (*1959*)
Microstegium nudum (Trin.) A. Camus (*1966*)
Pennisetum alopecuroides (L.) Sprengel (*1948*)

CYPERACEAE

Bulbostylis densa (Wallich) Hand.-Mazz. (*1969*)

ZINGIBERACEAE

Zingiber mioga (Thunb.) Roscoe (*2022*)

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B. B.
UNIVERSITY OF CALIFORNIA
BOTANICAL GARDEN
BERKELEY, CALIFORNIA 94720
Present address:
CALIFORNIA ACADEMY OF SCIENCES
GOLDEN GATE PARK
SAN FRANCISCO, CALIFORNIA 94118

D. E. B.
CARNEGIE MUSEUM OF NATURAL HISTORY
4400 FORBES AVENUE
PITTSBURGH, PENNSYLVANIA 15213
Present address:
HARVARD UNIVERSITY HERBARIA
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

S. A. S.
THE ARNOLD ARBORETUM OF
HARVARD UNIVERSITY
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS
02138

SYSTEMATICS OF HOLOGRAPHIS (ACANTHACEAE)

Thomas F. Daniel

Mexican Acanthaceae have received little taxonomic attention since Standley's treatment included in his *Trees and Shrubs of Mexico* (1926). As a result of field work associated with several floristic projects and the efforts of numerous individual collectors, the number of collections of Mexican Acanthaceae has greatly increased during the five decades since Standley's flora was published. However, there have been no comprehensive studies of *Holographis* or of the genera here considered congeneric with it. Work on these genera has been limited to regional floristic treatments and descriptions of new taxa.

In the present treatment, the relationships of two genera recognized by Standley and subsequent workers and a third, more recently described genus are discussed. Both *Berginia* Harvey ex Bentham & Hooker and *Lundellia* Leonard are considered to be congeneric with the older genus *Holographis* Nees. In addition to the new combinations in *Holographis,* three species from Mexico are described as new to science. This study also presents information on aspects of the ecogeography and phenology of the species.

Holographis comprises ten species of shrubby perennials that are confined to arid and semiarid habitats in Mexico. Most species are restricted in their distribution and are known from relatively few collections. The genus is characterized by the following combination of characters: spicate inflorescences, a five-parted calyx, a relatively small, strongly zygomorphic corolla, four monothecous stamens of approximately equal length, pubescent thecae that lack any appendages, a short staminode, and an ellipsoid capsule bearing four seeds. In addition, the plants lack cystoliths, and all but three of the species have whorled leaves.

TAXONOMIC HISTORY AND INTRAFAMILIAL RELATIONSHIPS

Based on a Mexican collection of Ehrenberg, Nees described the genus *Holographis* and the species *H. ehrenbergiana* Nees in the supplement to his treatment of the Acanthaceae in De Candolle's *Prodromus* (1847). He placed the genus in tribe Gendarusseae subtribe Gendarusseae "section" Pseudo-Aphelandreae and noted affinities with *Hemigraphis* Nees. Bentham and Hooker (1876) described the genus *Berginia* based on a Coulter collection from North America. The genus was placed in tribe Justicieae subtribe Asystasieae, and affinities with *Stenandrium* Nees were noted. Bentham and Hooker did not see any material of *Holographis,* but based on Nees's description they included that genus in tribe Justicieae subtribe Eujusticieae, where it was grouped with

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Aphelandra R. Br. and *Geissomeria* Lindley. In 1885 Asa Gray described *Pringleophytum* A. Gray from a Pringle collection from Sonora, Mexico, noting an alliance between his genus and *Holographis*. Brandegee (1889) suggested that *P. lanceolatum* A. Gray and *B. virgata* Harvey ex Bentham & Hooker were conspecific. Rose (*in* Vasey & Rose, 1890) described a second species of *Berginia, B. palmeri* Rose, and confirmed Brandegee's notion that *P. lanceolatum* and *B. virgata* were the same species. Lindau (1895) provided accounts of both *Holographis* and *Berginia* in his influential treatment of the family in *Die Natürlichen Pflanzenfamilien*. He placed both genera in subfam. Acanthoideae tribe Aphelandreae, which included members of the family that have a corolla imbricate in bud and with an upper lip, an androecium consisting of four monothecous stamens, and typical Spaltenpollen. *Holographis* and *Neriacanthus* Bentham were distinguished from other genera of the Aphelandreae (including *Berginia*) largely by the presence of a staminode. *Berginia* was also reported to have an unusual pollen type with three pores, each flanked by two furrows. Lindau's conception of *Berginia* was probably based on a misidentified specimen, since the genus has a staminode and tricolpate pollen.

In 1906 Brandegee described an unusual plant from the Chihuahuan Desert as *Holographis ilicifolia* Brandegee, but he was uncertain of its generic position. Subsequently, two additional species of *Holographis* (*H. pallida* Leonard & Gentry and *H. parayana* Miranda) and a species and a variety of *Berginia* (*B. hintonii* Leonard and *B. virgata* var. *glandulifera* Leonard & Morton) have been described. Leonard and Gentry (*in* Gentry, 1948) noted that *H. pallida* might eventually prove worthy of generic status due to the apparent uniqueness of its connivent anthers. They also noted the similarity of this species to species of *Berginia* and doubted whether the two genera could be kept separate. In 1959 Leonard described the genus *Lundellia* from southwestern Mexico. He claimed that its closest affinity was with the large American genus *Aphelandra*.

Bremekamp (1965) suggested revisions of tribes and subtribes within the family. Although he did not list the genera that comprise his subfamilies and tribes, if one uses his scheme, the species under consideration in this study would be included in subfam. Acanthoideae tribe Aphelandreae, which contains members of the family having four monothecous stamens, two ovules per ovary cell, a distinctly bilabiate corolla, and prolate, tricolpate pollen (except in *Stenandrium* subg. SPHAEROSTENANDRIUM), but lacking cystoliths. According to Bremekamp, this tribe is confined to the neotropics.

The closest relatives of *Holographis*, and the only other members of Lindau's Aphelandreae that occur in Mexico, are *Stenandrium* and *Aphelandra*. In Mexico these three genera can be distinguished by the following key:

1. Corolla subactinomorphic, lobes homomorphic; plants often acaulescent. .... *Stenandrium*.
1. Corolla strongly bilabiate, lobes heteromorphic; plants rarely acaulescent.
  2. Corolla orange, red, or purple (yellow in *A. verticillata*), 30–70 mm long. ...... *Aphelandra*.
  2. Corolla yellow, pink, rose-purple, or white, 7–18 mm long. ...... *Holographis*.

Holographis appears to be rather closely related to *Aphelandra*. There is no known substantial morphological character that invariably separates them.

Indeed, the two genera show some of the same trends (e.g., whorled leaves and spinose-toothed laminae), although they are usually readily distinguishable by a suite of characters. In *Aphelandra* the bracts are often brightly colored, the length of the corolla can reach 75 mm, and a staminode is rarely present (Wasshausen, 1975). In addition, *Aphelandra* is primarily a genus of damp habitats, with a center of diversity in South America. Only ten species are known to occur in Mexico (Wasshausen, 1975), and these are largely restricted to the wetter habitats in the southern part of the country. In contrast, *Holographis* does not have colored bracts, the length of the corolla reaches only 18 mm, and a staminode is always present. The plants are restricted to Mexico, where they occur in arid and semiarid associations throughout the country.

It is tempting to suggest that *Holographis* represents an evolutionarily specialized line (adapted for the northern desert regions into which it radiated) of some part of the large and variable genus *Aphelandra* or its ancestor. Some of the differences between the genera may have arisen in response to (or may be maintained because of) the apparent differences in pollination mechanisms. The small, usually pale-colored flowers that contain little nectar (as observed in *H. ilicifolia* and *H. argyrea*) suggest that *Holographis* is pollinated by a small bee or a fly. In contrast, the large, nectar-yielding, usually reddish flowers of *Aphelandra* are commonly hummingbird pollinated (Wasshausen, 1975).

MORPHOLOGY

HABIT. Plants of *Holographis* are erect, often intricately branched subshrubs or shrubs to 2 m tall, arising from a stout, woody base. Variation in habit due to exposure is particularly observable in specimens of *H. ilicifolia* and *H. ehrenbergiana*. Exposed or drought-induced forms tend to be compact shrubs with small leaves and close nodes.

STEMS. The epidermis of the persistent, woody stems frequently exfoliates in strips, exposing a whitish new surface. The younger stems are greenish or purplish to silvery white and are usually subquadrate in cross section. The surface is smooth, soon becoming conspicuously fluted, and is variably pubescent.

LEAVES. The leaves of *Holographis* are either opposite (subopposite in some individuals) or whorled, depending on the species. Seven species (*H. ilicifolia, H. ehrenbergiana, H. pueblensis, H. anisophylla, H. pallida, H. hintonii,* and *H. parayana*) have whorled leaves, with four at each node. *Holographis tamaulipica, H. argyrea,* and *H. virgata* have opposite leaves. In *H. pueblensis* the lower leaves are sometimes opposite or subopposite, and the upper leaves are whorled. The leaves are sessile or petiolate, simple, and usually entire. The leaves of *H. ilicifolia* are unusual in their chartaceous texture and spinose-toothed margins. The lamina varies from lanceolate through ovate, elliptic, and orbicular to obovate and is 3–64 by 2–28 mm.

The venation of all species of *Holographis* except *H. ilicifolia* is brochidodromous; that of *H. ilicifolia* is craspedodromous. In his study of leaf architecture in the Acanthaceae, Sreemadhaven (1976) noted the occurrence of both of these venation types in the Aphelandreae and considered pinnate craspedodromy to be derived from the pinnate-camptodromous condition.

The leaves tend to have trichomes similar to those of the stem from which they arise, but dendroid trichomes are present on the unfolding leaves of *Holographis argyrea.*

VESTITURE. *Holographis* has both glandular and eglandular trichomes. The latter are more common, and when glandular trichomes occur, they are usually intermixed with eglandular ones. Trichomes of the vegetative axes are eglandular, 0.05–1 mm long, and erect to flexuose, retrorse, or ascendant. Depending on the species, the calyxes and the inflorescence axes, bracts, and bractlets can have glandular trichomes in addition to eglandular ones. The capitate glandular trichomes are 0.05–0.5 mm in length. Trichomes can also occur on most parts of the flowers, fruits, and seeds. Those of the seeds are unusual in being dendroid, often with circinate branches. Branched trichomes are not usually found on other parts of the plant.

INFLORESCENCES. The inflorescences are axillary or terminal bracteate spikes (usually reduced to two flowers in *Holographis ehrenbergiana*) to 15 cm long. The spikes are congested, erect, and relatively short (1–6 cm long) in most species, but they are often loose, lax, and longer in others (especially taxa in the *H. virgata* complex). The flowers are sessile in the axil of two isomorphic bractlets and a bract and are opposite (alternate in *H. ilicifolia*) at the nodes of the inflorescence axis.

FLOWERS. The calyx is gamosepalous, five parted, and radially symmetrical. The tube is shorter than the homomorphic lobes. The calyx is fairly constant in length within a species, and its outer surface is often glandular.

The corolla is gamopetalous, pentamerous, and bilaterally symmetrical. It varies from yellow and white to pinkish and purplish, often with colorful markings. The orientation of the corolla varies from horizontal (e.g., in *Holographis pallida, H. parayana,* and *H. tamaulipica*) to erect (e.g., in *H. pueblensis, H. argyrea,* and *H. ehrenbergiana*). The tube is usually shorter than the limb and is slightly ampliate toward the apex (except in *H. argyrea*). The limb is bilabiate, the upper lip with two petal lobes that are fused for most or all of their length, and the lower lip with three large, basally fused lobes. Two prominent ridges are often evident in the center of the lower lip. In bud the petal lobes are imbricate, with the upper lip innermost, concealed by the lateral and central lobes of the lower lip; the lower-central lobe is outermost. The corollas of most species have eglandular trichomes on the outer surface, but those of *H. parayana, H. anisophylla,* and *H. hintonii* have glands as well. The corolla of *H. anisophylla* is somewhat unusual in having glands on the inner as well as the outer surface; that of *H. tamaulipica* is glabrous on the outer surface, with the inner surface usually conspicuously pubescent along the central lobe of the lower lip and/or near the junction of the corolla and the filaments.

The androecium consists of four epipetalous stamens and a staminode. The staminode is a short, filamentlike projection arising on the dorsal side of the corolla between the posterior pair of stamens; it lacks a theca, may be either glabrous or pubescent, and is 0.1–1.3 mm long. In most species the staminode emerges from the corolla at or about the same position as the filaments, although in *Holographis ilicifolia* it arises from the corolla up to 2 mm above the insertion of the filaments. The filaments of the fertile stamens emerge from the corolla near the apex of the tube and are either glabrous or pubescent. The anthers are monothecous and pubescent. The four thecae are frequently connivent at their apices and are basally rounded, lacking any appendages.

Pollen of at least one individual of each species (except *Holographis anisophylla*) was examined with a scanning electron microscope and/or a light microscope for shape, size, and sculpturing. Fresh pollen grains are prolate and generally uniform in size, with polar diameter (27.5–)35–40(–45) μm and equatorial diameter (17.5–)22.5–27.5(–30) μm. The grains are 1.3 to 1.6 times longer than wide. FIGURE 1 illustrates some of the variation in pollen of species of *Holographis*. The micrographs show that the grains are tricolpate. The colpi are often bifurcate near the poles, and the bifurcations from each colpus can fuse with those of the other colpi below the poles.

The gynoecium consists of a bicarpellate, superior ovary, a compound style, and usually two short stigma lobes. The ovary sits on a cuplike, fleshy disc. The style is filiform for most of its length but is conspicuously flared near the apex in some species. The presence or absence of trichomes on the style is usually constant for a species, but the styles of *Holographis pallida* and *H. virgata* can be either glabrous or pubescent. The stigma is either distinctly or inconspicuously bilobed, with the lobes often asymmetric.

FRUITS. The ovary develops into an indurate, two-valved capsule that dehisces explosively when mature. The capsule is ellipsoid in shape, splits to the base, and has no stalk; its outer surface is either glabrous or pubescent. The seed-bearing retinacula are hooklike and subequally inserted on the inner capsule wall. The seeds (up to four per capsule) are laterally flattened, suboval in shape, and either glabrous or pubescent. When present, the trichomes on the seeds are dendroid.

ECOGEOGRAPHY AND PHENOLOGY

Holographis is endemic to Mexico, from Baja California and northwestern Sonora, eastward to Tamaulipas, and southward to central Chiapas (MAPS 1, 3). Despite the extensive range of the genus in Mexico, most of the species have restricted distributions and are known from relatively few collections. *Holographis hintonii* and *H. anisophylla* are known only from the holotype, and *H. argyrea, H. tamaulipica,* and *H. pueblensis* are known from only two localities. *Holographis ehrenbergiana* and *H. virgata* have larger ranges, however, and can be common in certain regions.

There is no concentration of species in any one region of Mexico; in fact, the species are mostly allopatric, the only exceptions being *Holographis ehrenbergiana, H. tamaulipica,* and *H. pueblensis,* which overlap in range. There does appear to be a correlation of species with many of the arid and semiarid regions of Mexico, usually one species per region. *Holographis ilicifolia* is restricted to the Chihuahuan Desert, *H. virgata* to the Sonoran Desert region, *H. pallida* to the thorn forest south of the Sonoran Desert, *H. tamaulipica* to

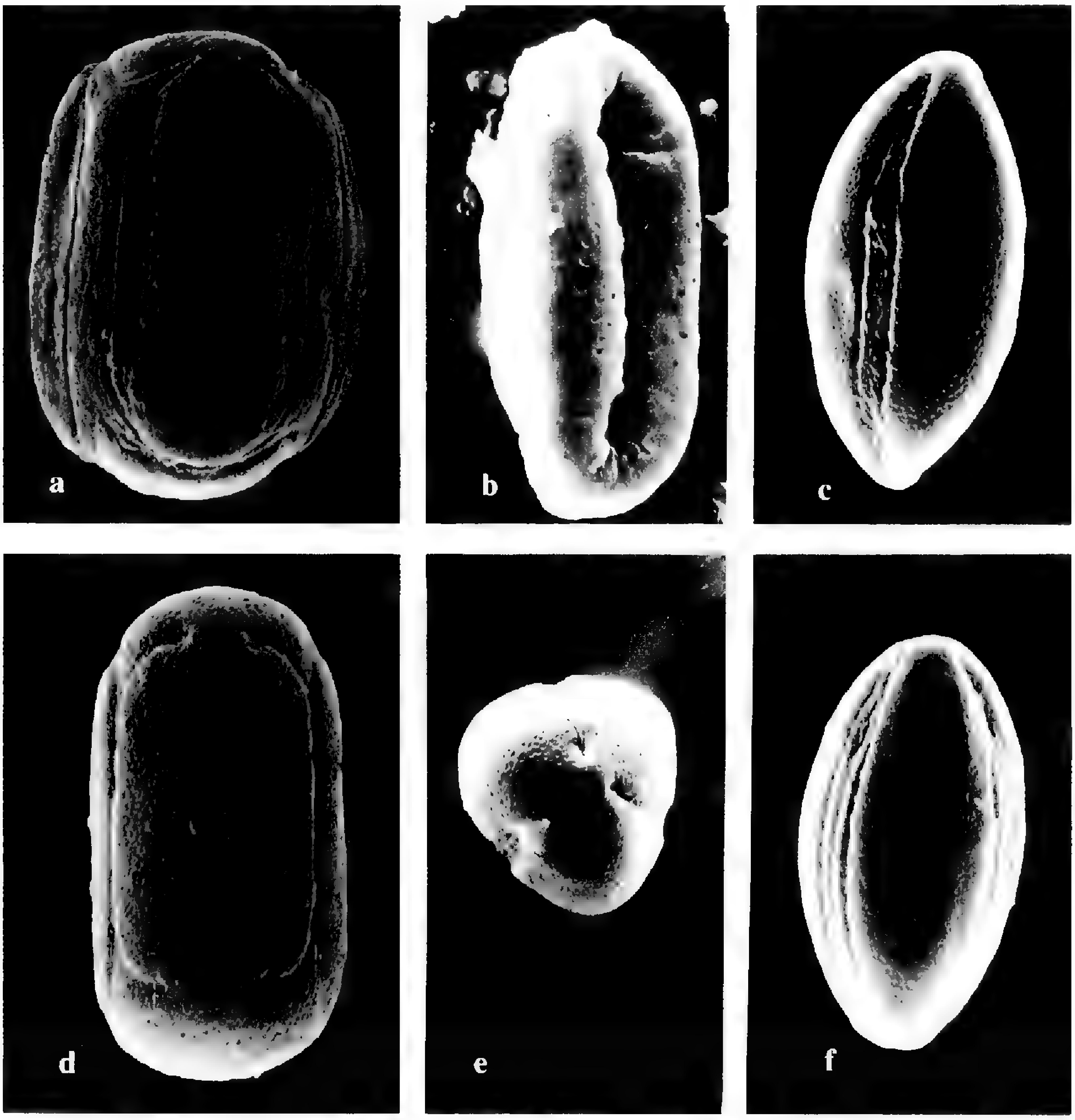
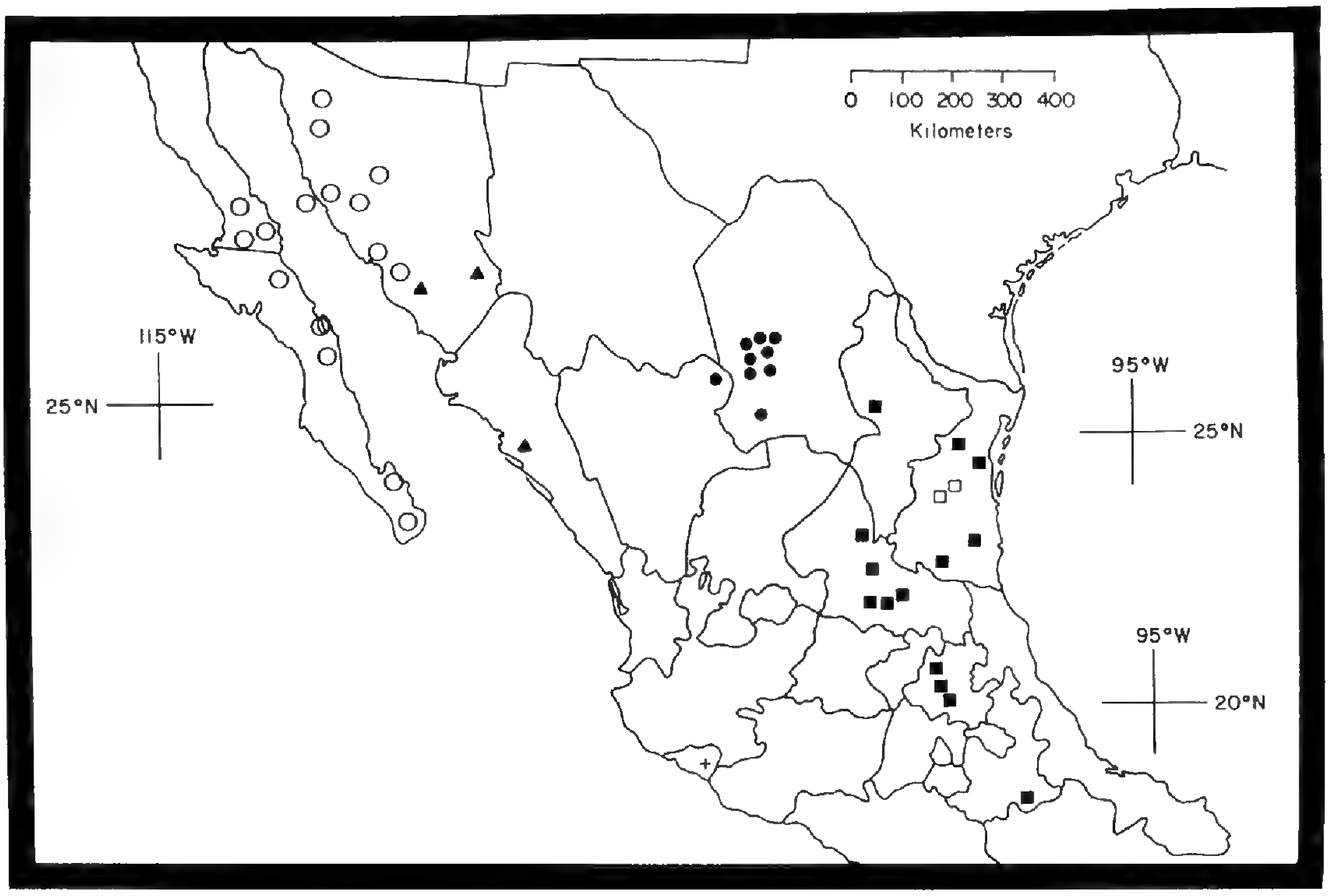


FIGURE 1. Variation in pollen of *Holographis* species: a, *H. virgata* subsp. *glandulifera* var. *glandulifera* (*Moran 3928*), equatorial view, × 775; b, *H. argyrea* (*T. Daniel 1242*), equatorial view, × 900; c, *H. ehrenbergiana* (*González Quintero 3581*), equatorial view, × 900; d, *H. pallida* (*H. Gentry 7022*), equatorial view, × 775; e, *H. ehrenbergiana* (*González Quintero 3581*), polar view, × 900; f, *H. ehrenbergiana* (*González Quintero 3581*), equatorial view, × 900.

the mesquite scrubland of central Tamaulipas, *H. pueblensis* to the arid Valley of Tehuacán, and *H. argyrea* and *H. hintonii* both to the arid tropical scrub of the Río Balsas Basin (however, their ranges are not known to overlap); *H. ehrenbergiana* is especially common in the Río Panuco relict desert region of Hidalgo but also occurs in the semiarid regions throughout northeastern Mexico. *Holographis parayana* and *H. anisophylla* both occur in regions of tropical deciduous forest that are somewhat isolated from the ranges of other species in the genus.

In his revision of the large genus *Aphelandra,* Wasshausen (1975) noted the pronounced endemism of many of the species and the wide scattering of individuals. *Holographis* appears to be closely related to *Aphelandra* (see discussion



Map 1. Northern and central Mexico, showing distribution of *Holographis anisophylla* (plus sign), *H. ehrenbergiana* (solid squares), *H. ilicifolia* (solid dots), *H. pallida* (solid triangles), *H. tamaulipica* (open squares), and *H. virgata* (circles).

under Taxonomic History and Intrafamilial Relationships) and shows the same phenomena. Additional, local species of *Holographis* will undoubtedly be discovered as botanical exploration of Mexico continues.

The species occur in several habitats at elevations from near sea level to 2000 meters. The plants are generally found in arid and semiarid associations including desert scrub, thorn forest, and tropical deciduous forest. The most frequent habitats are on exposed rocky slopes and along gravelly washes and arroyos.

Only *Holographis ilicifolia, H. ehrenbergiana,* and *H. virgata* are known from sufficient collections to determine their flowering periodicity adequately. Although both *H. ilicifolia* and *H. ehrenbergiana* have been collected during most months of the year, the majority of specimens of each species were taken during the period from July through September, corresponding to the summer rainy season in the Chihuahuan Desert region and the dry regions of northeastern Mexico where these species occur. Members of the *H. virgata* complex have been collected in flower during every month except July, August, and September, although peak flowering occurs from March through May, corresponding to the end of the season of winter rains in the western section of the Sonoran Desert. The few collections of the other species of *Holographis* suggest that *H. pallida, H. hintonii, H. tamaulipica,* and *H. parayana* flower predominantly January through April, *H. pueblensis* in June and July, *H. argyrea* in October and November, and *H. anisophylla* in November and December.

Fruiting collections are not known for all of the species, and fruits and flowers are seldom found together on specimens of those species whose fruits are known. It appears that fruiting begins several weeks after flowering has started.

TAXONOMIC TREATMENT

Holographis Nees in DC. Prodr. **11**: 728. 1847. TYPE SPECIES: *Holographis ehrenbergiana* Nees.

Berginia Harvey ex Bentham & Hooker, Gen. Pl. **2**: 1096. 1876. TYPE SPECIES: *B. virgata* Harvey ex Bentham & Hooker.

Pringleophytum A. Gray, Proc. Amer. Acad. Arts **20**: 292. 1885. TYPE SPECIES: *P. lanceolatum* A. Gray.

Lundellia Leonard, Wrightia **2**: 1. 1959. TYPE SPECIES: *L. argyrea* Leonard.

Erect to spreading subshrubs to shrubs to 2 m tall, arising from stout, woody base. Older stems woody, pubescent, or glabrate; younger stems green, purplish, or silvery white, terete to quadrate to ellipsoid in cross section, the surface smooth to striate to fluted, pubescent, often densely so. Leaves opposite (rarely subopposite) or whorled (4 per node), sessile to petiolate; lamina linear-lanceolate to obovate, the margin entire (spinose toothed in *H. ilicifolia*), flat or revolute, the surfaces pubescent, often sparsely so, with abaxial surface punctate in some species. Inflorescences axillary or terminal spikes (usually reduced to 2 flowers in *H. ehrenbergiana*); flowers sessile, opposite (alternate in *H. ilicifolia*) along spike axis, subtended by 2 paired, isomorphic bractlets and a bract; bracts and bractlets usually similar in shape, often of different relative lengths. Calyx deeply 5-lobed, lobes homomorphic; corolla yellow or white to purplish or pinkish, bilabiate, pubescent (glabrous in *H. tamaulipica*) on outer surface, the tube usually shorter than the lips, usually ampliate above, the upper lip bilobed, the lower lip trilobed, with lobes spatulate, central lobe usually conspicuously larger and extending beyond lateral ones and usually with 2 prominent ridges down middle; stamens 4, included or slightly exserted and appressed to upper lip, the filaments glabrous or pubescent, the anthers monothecous, with thecae introrse, pubescent, often connivent; staminode short, borne between posterior pair of stamens, glabrous or pubescent, theca lacking; style terminal, filiform, glabrous or pubescent, either flared near apex into distinct, equal or unequal stigmatic lobes or slightly flared and with stigmatic lobes inconspicuous. Capsules brown, ellipsoid, bilocular, splitting to base, glabrous or pubescent on outer surface; retinacula 4 per capsule, hooklike. Seeds 4 per capsule (or fewer by abortion), laterally flattened, suboval, surface and margins glabrous or pubescent.

DISTRIBUTION. Mexico: Baja California Norte, Sonora, Coahuila, Nuevo León, and Tamaulipas, southward to Chiapas.

KEY TO THE SPECIES OF HOLOGRAPHIS

1. Leaves opposite (rarely subopposite).
    2. Cauline trichomes ascendant-appressed; inflorescence spikes axillary; bracts 2–3 mm long, glabrous; calyx 4–5 mm long; corolla glabrous on outer surface. . . . . 1. *H. tamaulipica*.
    2. Cauline trichomes straight, flexuose or retrorse; inflorescence spikes terminal on branches; bracts 3–8 mm long, pubescent; calyx 5–8 mm long; corolla pubescent on outer surface.

3. Cauline trichomes 0.05–1 mm long; corolla reddish pink, 9–14 mm long; stamens 2.8–5 mm long; Sonoran Desert region. . . . . 2. *H. virgata.*
3. Cauline trichomes 0.05 mm long or less; corolla yellow, 7–9.5 mm long; stamens 1.5 mm long; Guerrero. . . . . 3. *H. argyrea.*

1. Leaves whorled, 4 per node (lower leaves of *H. pueblensis* sometimes opposite to subopposite).
    4. Leaves orbicular, 0.8–1.3 times longer than wide, margin spinose toothed; bracts alternate; Chihuahuan Desert region. . . . . 4. *H. ilicifolia.*
    4. Leaves lanceolate to obovate, 1.5–4.5 times longer than wide, margin entire; bracts opposite; not of Chihuahuan Desert region.
        5. Corolla 8–10 mm long, glandular on outer surface; stamens 2.5–3.5 mm long.
            6. Cauline trichomes ascendant-appressed, 0.1–0.3 mm long; bracts triangular to lance-subulate, eglandular, emucronate; calyx 2–3 mm long; style 5–6 mm long; ovary glabrous. . . . . 5. *H. parayana.*
            6. Cauline trichomes retrorse, 0.05–0.1 mm long; bracts lance-ovate to orbicular, glandular, mucronate; calyx 4–5 mm long; style 3.5–4 mm long; ovary pubescent.
                7. Inflorescence axis glandular-pubescent with glandular trichomes 0.05 mm long and straight eglandular trichomes 0.05–0.1 mm long; bracts lance-ovate to ovate, 2.5–3 mm long; bractlets lance-ovate to ovate, 2–2.8 mm long; stamens 2.5–3 mm long; staminode pubescent. . . . . .6. *H. anisophylla.*
                7. Inflorescence axis eglandular with crooked, interwoven trichomes to 0.8 mm long; bracts broadly ovate to orbicular, 1.5–2 mm long; bractlets lanceolate, 1.5–2 mm long; stamens 3–3.5 mm long; staminode glabrous. . . . . 7. *H. hintonii.*
        5. Corolla 10–18 mm long, pubescent with eglandular trichomes on outer surface; stamens 3.5–11 mm long.
            8. Cauline trichomes retrorse, 0.05–0.2 mm long; laminar margin flat; bracts mucronate; corolla white to lavender, 10–12 mm long, horizontal at anthesis; style 5.3–6 mm long. . . . . 8. *H. pallida.*
            8. Cauline trichomes straight to ascendant-appressed, 0.1–0.7 mm long; laminar margin revolute; bracts emucronate; corolla yellow, 12–18 mm long, vertical at anthesis; style 12–16 mm long.
                9. Inflorescence spikes many flowered, to 4.5 cm long; bracts 6.5–11 by 1.5–2 mm; calyx 7–10.5 mm long. . . . . 9. *H. pueblensis.*
                9. Inflorescence spikes to 2 cm long, usually reduced to 2 flowers; bracts 1.5–5 by 0.5–1 mm; calyx 3.5–6 mm long. . . . 10. *H. ehrenbergiana.*

1. **Holographis tamaulipica** T. F. Daniel, sp. nov. FIGURE 2.

Frutex erectus. Caules juniores substriati pubescentes trichomatibus eglandulosis 0.2–0.6 mm longis. Folia opposita; laminae lanci-ovatae vel ellipticae, (15–)25–64 mm longae, (6–)9–28 mm latae, 2–4-plo longiores quam latiores, marginibus revolutis ciliatis. Inflorescentia spicata; bracteae triangulatae vel ovatae, 2–3 mm longae, 1.5–2 mm latae; bracteolae lanceolatae, 1.5–2.2 mm longae. Calyx 4–5 mm longus; corolla 9–11 mm longa, extus glabra; stamina 3.5–4 mm longa filamentis 2–2.5 mm longis, pubescentibus; staminodium 0.2–0.3 mm longum, pubescens; stylus 6–6.5 mm longus, glaber. Capsula 9 mm longa, glabra.

Erect shrub. Older stems pubescent or glabrate; younger stems green, terete in cross section, the surface somewhat striate, evenly pubescent, the trichomes

FIGURE 2. *Holographis tamaulipica* (from holotype): a, habit, × 0.6; b, spike, × 3.5; c, dissected flower, × 4; d, gynoecium, × 4.5.

eglandular, ascendant-appressed, 0.2–0.6 mm long. Leaves opposite, ascendant to horizontal; petiole to 10 mm long, pubescent; lamina lance-ovate to elliptic, attenuate at base, acute at apex, (15–)25–64 by (6–)9–28 mm, 2 to 4 times longer than wide, the margin entire, revolute, ciliate with erect to flexuose trichomes 0.2–0.8 mm long, the surfaces subglabrous or sparsely pubescent. Inflorescences axillary or terminal, pedunculate spikes to 9 cm long; peduncles 1–9 mm long; axes pubescent with erect to ascendant trichomes 0.05–0.2 mm long; flowers opposite at spike nodes; lower bracts (rarely absent) sterile; upper bracts fertile, triangular to ovate, 2–3 by 1.5–2 mm, submucronate to mucronate at apex, outer surface glabrous, margin often ciliate; bractlets lanceolate, shorter than or approximately same length as subtending bract, 1.5–2.2 by 0.7–1 mm, pubescent like bracts. Calyx 4–5 mm long, the lobes lance-subulate, mucronate at apex, pubescent like bracts; corolla white (label data), horizontal at anthesis, 9–11 mm long, glabrous on outer surface, the tube 4–5 mm long, ampliate above, the upper lip 3.5–5 mm long, with lobes 2–3 mm long, the lower lip 5–6 mm long, with lobes spatulate, 3.5–4.5 by 1.5–2 mm; stamens 3.5–4 mm long, the filaments 2–2.5 mm long, pubescent, the thecae 1.5–2 mm long, pubescent; staminode 0.2–0.3 mm long, pubescent; style 6–6.5 mm long, glabrous, flared at apex, the stigma unequally bilobed, with longer lobe to 0.5 mm long. Capsules 9 mm long, 3.8 mm in diameter, glabrous. Seeds not seen.

TYPE. Mexico, Tamaulipas, vicinity of Victoria, ca. 320 m, 1 Feb.–9 April 1907, *Palmer 135* (holotype, GH!; isotype, F!).

This species is known only from the type specimens and one additional collection, both of which were collected near Victoria, Tamaulipas (MAP 1) in the early spring. The paratype was collected on a shaded limestone ledge in oak woods at 1200 meters.

Holographis tamaulipica is unique among the known species of *Holographis* in having a glabrous corolla. It does not appear to be very closely related to the other two species with opposite leaves. In cauline pubescence, flower size, and corolla orientation it resembles *H. parayana.*

ADDITIONAL SPECIMEN EXAMINED. **Mexico.** TAMAULIPAS: 12 mi from river at Victoria on road to Jamauve, *Moore & Valiente M. 6159A* (US).

2. **Holographis virgata** (Harvey ex Bentham & Hooker) T. F. Daniel, comb. nov.

Berginia virgata Harvey ex Bentham & Hooker, Gen. Pl. **2:** 1097. 1876. TYPE: "California incola," without date, *Coulter 603* (holotype, K!; isotypes, GH!, K (2 sheets)!).
Pringleophytum lanceolatum A. Gray, Proc. Amer. Acad. Arts **20:** 293. 1885. TYPE: Mexico, Sonora, rocky hills 50 mi below Altar and 30 mi from Gulf of California, 1884, *Pringle s.n.* (holotype, GH; isotypes, F!, NY!, US!).

Erect shrub to 2 m tall. Older stems often whitish, pubescent or glabrate; younger stems pale green, soon becoming either whitish or purplish, subquadrate to quadrate in cross section, the surface striate, soon becoming conspicuously fluted, evenly pubescent, with trichomes eglandular and erect, flexuose, or retrorse, 0.05–0.7(–1) mm long. Leaves opposite (or subopposite), ascendant, sessile to petiolate; petiole (if present) to 5 mm long, pubescent; lamina linear-lanceolate to obovate, acute to attenuate at base, acute to rounded (rarely emarginate) at apex, (4–)6–46 by 2–26 mm, 1.1 to 9.2 (to 17) times longer than wide, the margin entire, flat to revolute, ciliate, the surfaces pubescent. Inflorescences terminal, loosely or densely bracteate spikes to 15 cm long; axes pubescent with eglandular trichomes or with mixture of eglandular and glandular trichomes; flowers opposite (to subopposite) at spike nodes; lower bracts (up to 6 series) often sterile, triangular to orbicular; upper bracts fertile, somewhat foliaceous, lance-ovate to ovate to elliptic to orbicular, 3–8 by 1.5–5 mm, usually pubescent like inflorescence axis; bractlets lance-subulate to linear to lanceolate, approximately equal to or shorter than subtending bract, 2–6 by 0.6–1.5 mm, pubescent with eglandular or mixture of eglandular and glandular trichomes. Calyx 5–8 mm long, the lobes lanceolate or oblanceolate, pubescent like bractlets; corolla reddish pink with white markings, 9–14 mm long, pubescent on outer surface with eglandular trichomes (rarely with glandular trichomes as well in subsp. *glandulifera* var. *glandulifera*), the tube 5–8 mm long, ampliate above, the upper lip (2.5–)3–5 mm long, with lobes 1.5–4 mm long, the lower lip 4–8 mm long, with lobes spatulate, 2.5–6 by 1.5–3.5 mm; stamens 2.8–5 mm long, the filaments 1.5–4 mm long, pubescent or nearly glabrous, the thecae 1.6–2.5 mm long, pubescent (anterior pair usually more densely so); staminode 0.5–0.8 mm long; style 5–7 mm long, glabrous or pubescent, flared at apex, the stigma subequally bilobed, 0.3–0.5 mm long. Capsules 7–12 mm long, 3–5 mm in diameter, pubescent or essentially glabrous, with trichomes often restricted to apex, eglandular, 0.05–0.3 mm long, the retinacula 1.5–2.5 mm long. Seeds obliquely cordate to widely elliptic, 2–3.5 by 2–3 mm, pubescent with dendroid trichomes to 0.3 mm long.

As treated in this study, *Holographis virgata* comprises three taxa formerly recognized in *Berginia.* The most perplexing problem remaining in *Holographis* is the status of these taxa from Baja California and Sonora. The geographic discontinuity between the eglandular northern populations and the glandular southern populations justifies their recognition at the rank of subspecies. Due to minor differences in pubescence and an apparent difference in habitat elevation among the southern populations, two varieties are recognized in the southern subspecies. I feel confident that these plants are all part of the same species. The infraspecific treatment presented here, however, may presuppose a greater degree of understanding of this complex than can be obtained from herbarium material alone. Although the differences in pubescence among the three taxa are clear and most specimens can be easily identified, the nature of these distinctions is subtle. Pubescence can be influenced by environmental factors. Field work in Baja California and cultivation of these plants in an experimental garden will undoubtedly increase our understanding of their relationships.

Key to the Infraspecific Taxa of *Holographis virgata*

1. Inflorescence axes, bracts, bractlets, and calyx eglandular (rarely with inconspicuous glands on bractlets and calyx); bractlets 0.6–1 mm wide; Sonora and Baja California north of lat. 28°N. .... 2a. *H. virgata* subsp. *virgata.*
1. Inflorescence axes, bracts, bractlets, and calyx conspicuously glandular; bractlets 1–1.5 mm wide; Baja California, mostly south of lat. 28°N.

2. Leaves and young stems scaberulous, with trichomes retrorse, 0.05–0.1 mm long; usually below 600 m alt. .... 2b. *H. virgata* subsp. *glandulifera* var. *glandulifera.*
2. Leaves and young stems hirtellous, with trichomes straight to flexuose, 0.1–1 mm long; usually above 600 m alt. ... 2c. *H. virgata* subsp. *glandulifera* var. *palmeri.*

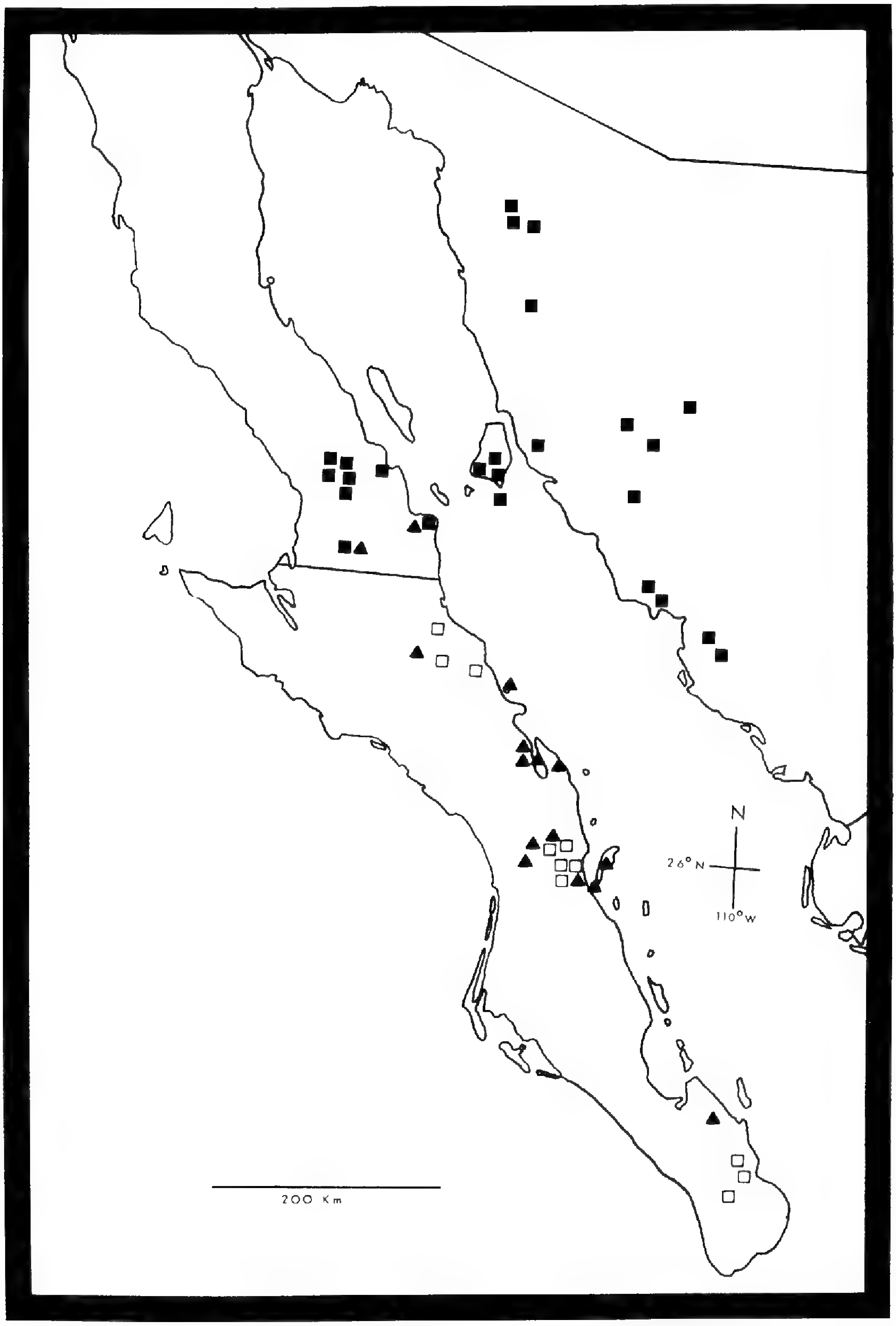
2a. **Holographis virgata** (Harvey ex Bentham & Hooker) T. F. Daniel subsp. **virgata**

Trichomes of younger stems erect to retrorse, 0.05–0.1 mm long. Leaves sessile or subsessile; lamina linear-lanceolate to lanceolate to elliptic (to obovate), (4–)7–43 by 2–9(–14) mm, (1.6 to) 3 to 17 times longer than wide. Inflorescence axes pubescent with eglandular, erect to retrorse trichomes 0.05–0.2(–0.5) mm long; bracts 1.5–3 mm wide, pubescent like inflorescence axis; bractlets 0.6–1 mm wide, pubescent like bracts (rarely also with scattered glandular trichomes to 0.2 mm long). Lower lip of corolla 5–8 mm long, lobes 4–6 by 2.5–3.5 mm. Capsule essentially glabrous to pubescent, trichomes often restricted to apex.

DISTRIBUTION AND HABITATS. Sonoran Desert of western and central Sonora and southern Baja California Norte (MAP 2); on gravelly slopes and along arroyos and washes, 15–1300 m alt.; with species of *Jatropha* L., *Pachycereus* (A. Berger) Britton & Rose, *Pachycormus* Cov. ex Standley, *Idria* Kellogg, *Larrea* Cav., *Opuntia* Miller, *Acacia* Miller, *Cercidium* Tulasne, *Simmondsia* Nutt., *Croton* L., and *Carnegiea* Britton & Rose.

FLOWERING AND FRUITING. Flowering October through June; fruiting simultaneously, more commonly during latter portion of flowering period.

REPRESENTATIVE SPECIMENS. **Mexico.** BAJA CALIFORNIA NORTE: Mina Desengaña, ca. 16 mi N of Punta Prieta, *H. Gentry & Cech 8887* (MEXU, MICH, US); ca. 22 mi from Bahía Los Angeles on road to San Borja, *H. Gentry & McGill 23313* (ASU, DES, MICH); 7 mi W of San Francisquito Bay, *Harbison 41665* (SD); Las Animas Bay, *I. Johnston 3509* (CAS, GH, NY, UC); Paredones, *Montufar 42* (ENCB); Agua de Higuera, *Moran 7956* (ARIZ, DS, MICH, SD, UC); Sierra San Borja, San Juan Mine, *Moran 8060* (DS, SD, UC); Turners Is., *Moran 13024* (SD, UC); Calmallí, *Purpus 56* (DS, F, NY, UC, US); 8 mi N of Mission San Borja, *Thorne & Henrickson 32677* (MICH); 3 mi S of Agua Higuera along road to Mission San Borja, *Wiggins & Wiggins 14830* (CAS, MEXU, MICH). SONORA: 12 mi NW of Hermosillo, *Abrams 13305* (DS, F); canyon back of Palma, 40 mi S of Hermosillo, *Abrams 13348* (DS); ca. 31 mi E of Punta Cirio between Puerto Libertad and Caborca, *Bowers & McLaughlin s.n.,* 13 April 1979 (ARIZ); 10 mi NW of Hermosillo, *C. Carter s.n.,* 13 April 1932 (MICH); near Guaymas, *Dawson 1075* (F, MICH); San Miguel de Horcasitas, *Eisen s.n.,* May 1892 (US); Picu Mts., Altar Distr., *H. Gentry 4479* (DES, MICH, MO); Sierra Cajon del Diable, *H. Gentry 11622* (MEXU, MICH); 22.2 mi N of Bahía Kino Nuevo, *Hastings & Turner 64-40* (ARIZ, DS, SD); 0.9 mi E of Pitiquito, *Hastings & Turner 64-58* (ARIZ, DS, SD); Guaymas, *I. Johnston 3114* (CAS, GH, US); Hermosillo, *Jones 22531* (MO); 8 mi NW of Caborca on road to Tajitos, *Keck 4059* (CAS, DS, F, MO, NY); near Pozo Cerna, *Long 62* (US); Tiburón Is., *Moran 4065* (DS, SD, UC); Guaymas, *Palmer 307* (GH); near Rancho Verruga, Distr. Altar, *Shreve 5823* (ARIZ, US); 15 mi NW of Caborca, *Shreve 7553* (ARIZ, F, MICH, MO, US); ca. 20 mi NE of Obregón, *Spaulding 75-3-12* (ARIZ); 8 mi ESE of Vicam along Hwy. 15, *Turner & Hastings 69-64* (ARIZ); 0.2 mi W of Rancho San Alfroso, *Turner & Duek 79-37* (ARIZ); Puerto Los Mochos, Rancho Los Mochos, 20.7 mi NE of Desemboque de San Ignacio, *Van Devender & Kearns s.n.,* 17 Feb. 1977 (ARIZ).



MAP 2. Northwestern Mexico, showing distribution of infraspecific taxa of *Holographis virgata:* subsp. *virgata* (solid squares), subsp. *glandulifera* var. *glandulifera* (solid triangles), subsp. *glandulifera* var. *palmeri* (open squares).

This is the most widely distributed and most variable subspecies of *Holographis virgata.* It occurs primarily to the north and east of the range of *H. virgata* subsp. *glandulifera,* but the two subspecies do come together in southern Baja California Norte near Calmallí (lat. 28°08′N, long. 113°24′W). At this locality Purpus collected specimens of *H. virgata* subsp. *virgata, H. virgata* subsp. *glandulifera* var. *glandulifera,* and intermediates. The intermediate plants on *Purpus 56* (UC) have sparsely glandular inflorescence axes, while other plants on the sheet have densely glandular (*H. virgata* subsp. *glandulifera* var. *glandulifera*) and eglandular (*H. virgata* subsp. *virgata*) axes. Duplicates of Purpus's collection at F and NY contain plants with varying degrees of glandularity. *Brandegee 443* from the Sierra de la Laguna in the Cape Region of Baja California Sur contains sprigs of *H. virgata* subsp. *virgata* and of *H. virgata* subsp. *glandulifera* var. *palmeri.* Although there is some variation among the sprigs of *H. virgata* subsp. *virgata* in the length of the pubescence on the inflorescences, the variation falls within the range normally encountered in that subspecies.

Annetta Carter, of the University of California (Berkeley) Herbarium, notes (*in litt.*) that during Brandegee's trip from Magdalena Bay to San Quintín in 1889, he was in the vicinity of Calmallí in late April. This was the only time he passed through the range of *Holographis virgata* subsp. *virgata.* She notes that at that time, Brandegee could have collected the material of *H. virgata* subsp. *virgata* as represented on *Brandegee 443.* While working on his collections of 1889 and 1890, he might have mixed material of the two subspecies.

Holographis virgata subsp. *virgata* shows considerable variation in the length of the eglandular pubescence on the inflorescence axes and in the amount of pubescence on the capsules. It can be distinguished from *H. virgata* subsp. *glandulifera* by the general absence of glandular trichomes on the inflorescence; however, in some individuals the bractlets and calyx can contain inconspicuous glands.

2b. **Holographis virgata** subsp. **glandulifera** (Leonard & Morton) T. F. Daniel, comb. et stat. nov., var. **glandulifera**

Berginia virgata var. *glandulifera* Leonard & Morton, Contr. Dudley Herb. **4:** 24. 1950. TYPE: Mexico, Baja California Sur, 32 mi S of Mulegé, 15 March 1935, *Shreve 7101* (holotype, US!; isotypes, ARIZ!, DS!, F!, MICH!).

Trichomes of the younger stems retrorse, 0.05–0.1 mm long. Leaves subsessile; petiole to 3 mm long; lamina lance-ovate to oblanceolate, 6–43 by 3–22 mm, 1.3 to 3.8 times longer than wide. Inflorescence axes pubescent with mixture of glandular and eglandular trichomes, the former 0.1–0.3 mm long, the latter erect to flexuose, 0.05–0.3 mm long; bracts (2–)2.5–5 mm wide, lower ones pubescent like leaves, upper ones pubescent like inflorescence axis; bractlets 1–1.5 mm wide, pubescent like inflorescence axis but usually with more numerous glands. Lower lip of corolla 4–5 mm long, lobes 3–4 by 1.5–3 mm. Capsules pubescent.

DISTRIBUTION AND HABITAT. Known from southern Baja California Norte, but more common in eastern and central Baja California Sur (MAP 2); rocky slopes, arroyos, and gravelly washes to about 600 m alt.; with *Lysiloma* Bentham, *Mimosa* L., *Jatropha, Bursera* Jacq. ex L., *Pachycereus, Lemaireocereus* Britton & Rose, *Ruellia* L., *Fouquieria* Kunth, and *Cyrtocarpa* Kunth.

FLOWERING AND FRUITING. Flowering November through May and into June; fruiting simultaneously, more commonly during latter portion of flowering season.

REPRESENTATIVE SPECIMENS. **Mexico.** BAJA CALIFORNIA NORTE: 20 mi W of Bahía San Francisquito, *Humphrey 6830a* (ARIZ); diggings at Calmallí, *Purpus 56, pro parte* (UC). BAJA CALIFORNIA SUR: Purísima to Comondú, *Brandegee s.n.,* 15 Feb. 1889 (UC); Comondú, *Brandegee s.n.,* 15 Feb. 1890 (F, GH); 12.4 km SE of La Paz on road to Los Planes, *A. Carter 2625* (DS, MEXU, MICH, SD, UC, US); vic. of Rancho Los Burros, E of Llanos de San Pedro, NE of Comondú, *A. Carter & Ferris 3430* (DS, MEXU, SD, UC); Arroyo Carrizal, E of Rancho El Horno (NE of San Xavier), *A. Carter & Ferris 3829a* (CAS, UC); S of Tinaja de Naucajoa, Cerros de Naucajoa (W of Llanos de San Juan), *A. Carter 4502* (UC); Puerto Escondido, *Dawson 1098* (F, MICH); Las Cuevitas below Comondú, *H. Gentry 4235* (DES, DS, MICH, MO); between San Ignacio and Los Martiles, *H. Gentry 7872* (ARIZ, DS, MICH, UC); San Nicholas Bay, *I. Johnston 3729* (CAS); Carmen Is., Puerto Ballandra, *I. Johnston 3820* (CAS, GH, NY, UC, US); Carmen Is., Ballandra Bay, *Moran 3928* (DS, SD, UC, US); San Marcos Is., Arroyo de los Chivos, *Moran 8999* (SD); Danzante Is., *Moran 9249* (SD); island in Conception Bay, *Rempel 197* (ARIZ), *208* (ARIZ); 14 mi S of Mulegé, *Shreve 7086* (ARIZ, F, GH, MICH, MO).

This variety resembles *Holographis virgata* subsp. *virgata* in the pubescence of the vegetative axis, and where the ranges of these taxa overlap, intermediates occur. In its distribution and in characters of inflorescence pubescence and bract width, this variety appears closer to *H. virgata* subsp. *glandulifera* var. *palmeri.* These latter taxa are distinguishable from each other by the relative lengths of the foliar and cauline trichomes and by the differences in elevation of their habitats.

2c. **Holographis virgata** subsp. **glandulifera** var. **palmeri** (Rose) T. F. Daniel, comb. et stat. nov.

Berginia palmeri Rose, Contr. U. S. Natl. Herb. **1:** 86. 1890. TYPE: Mexico, Baja California Sur, Santa Rosalía, 15 March 1890, *Palmer 272* (holotype, US!; isotypes, A!, DS!, F!, GH!, NY!).

Trichomes of the younger stems erect to flexuose, 0.1–0.7(–1) mm long. Leaves sessile to petiolate; petiole to 5 mm long; lamina lance-ovate to obovate, (6–)11–46 by (4–)7–26 mm, 1.1 to 3.3 times longer than wide. Inflorescence axes pubescent with mixture of eglandular and glandular trichomes, the former 0.2–1 mm long, the latter 0.2–0.5 mm long; bracts 2.5–4.5 mm wide, pubescent like inflorescence axis; bractlets 1–1.5 mm wide, pubescent like inflorescence axis although glandular trichomes usually more numerous. Lower lip of corolla 5–6.5 mm long, lobes 2.5–4 by 2–3 mm. Capsules pubescent.

DISTRIBUTION AND HABITAT. Eastern Baja California Sur (especially common in and around Sierra de la Giganta (MAP 2)); among rocks on slopes and in arroyos above 600 m alt.; with *Jatropha, Hechtia* Klotzsch, *Pachycormus, Franseria* Cav., *Lysiloma, Lemaireocereus, Colubrina* Rich. ex Brongn., *Bur-*

sera, Ficus L., *Erythrina* L., *Agave* L., *Bernardia* Miller, *Viguiera* Kunth, and *Croton.*

FLOWERING AND FRUITING. Flowering October through June; fruiting predominantly March through June.

REPRESENTATIVE SPECIMENS. **Mexico.** BAJA CALIFORNIA SUR: Sierra de Laguna, *Brandegee 443* (UC); Arroyo Carrizal, E of Rancho El Horno (NE of San Xavier), *A. Carter & Ferris 3819, pro parte* (CAS, MEXU, UC, US); N slope of Pilón de las Parras, W of Loreto, *A. Carter & Sharsmith 4215* (CAS, F, MO, NY, UC, US); Sierra de la Giganta, S of La Puerta, W end of Valle de los Encinos (S side of Cerro Giganta), *A. Carter & Reese 4574* (CAS, MEXU, UC, US); Sierra de la Giganta, Mesa de San Geronimo, N of Rancho Viejo, *A. Carter 5131* (CAS, GH, MICH, SD, UC, US); 5 mi S of San Bartolo, *Gallagher 139* (ASU); Sierra Giganta above Pto. Escondido, *H. Gentry 3762* (A, ARIZ, DES, MICH, MO, UC); Volcán las Tres Vírgenes, *Moran 20459* (SD); La Ciénega Arroyo, Distr. of Buena Vista, *Peters 206* (UC); 8 mi E of pass of Tres Vírgenes Peak, *Shreve 7051a* (ARIZ); El Purgatorio grade W of Santa Rosalía, *Wiggins & Wiggins 18206* (CAS, DS, MEXU).

Most (if not all) of the specimens from the vicinity of the Sierra de la Giganta were collected above 600 meters in elevation; however, *Peters 206* (from the Cape Region) was collected at about 33 m alt. Ms Carter notes (*in litt.*), "In the Cape Region, some plants occur both at low and higher altitudes whereas to the north (Sierra de la Giganta) the same taxon is restricted to higher altitudes. A case in point is *Jatropha vernicosa* which occurs above 2000 feet in the Sierra de la Giganta, but in the Cape Region it grows on coastal plain as well as at higher elevations in the mountains." Peters's specimen is unusual in having relatively few glands in the inflorescence, but it has the long, eglandular trichomes characteristic of this variety.

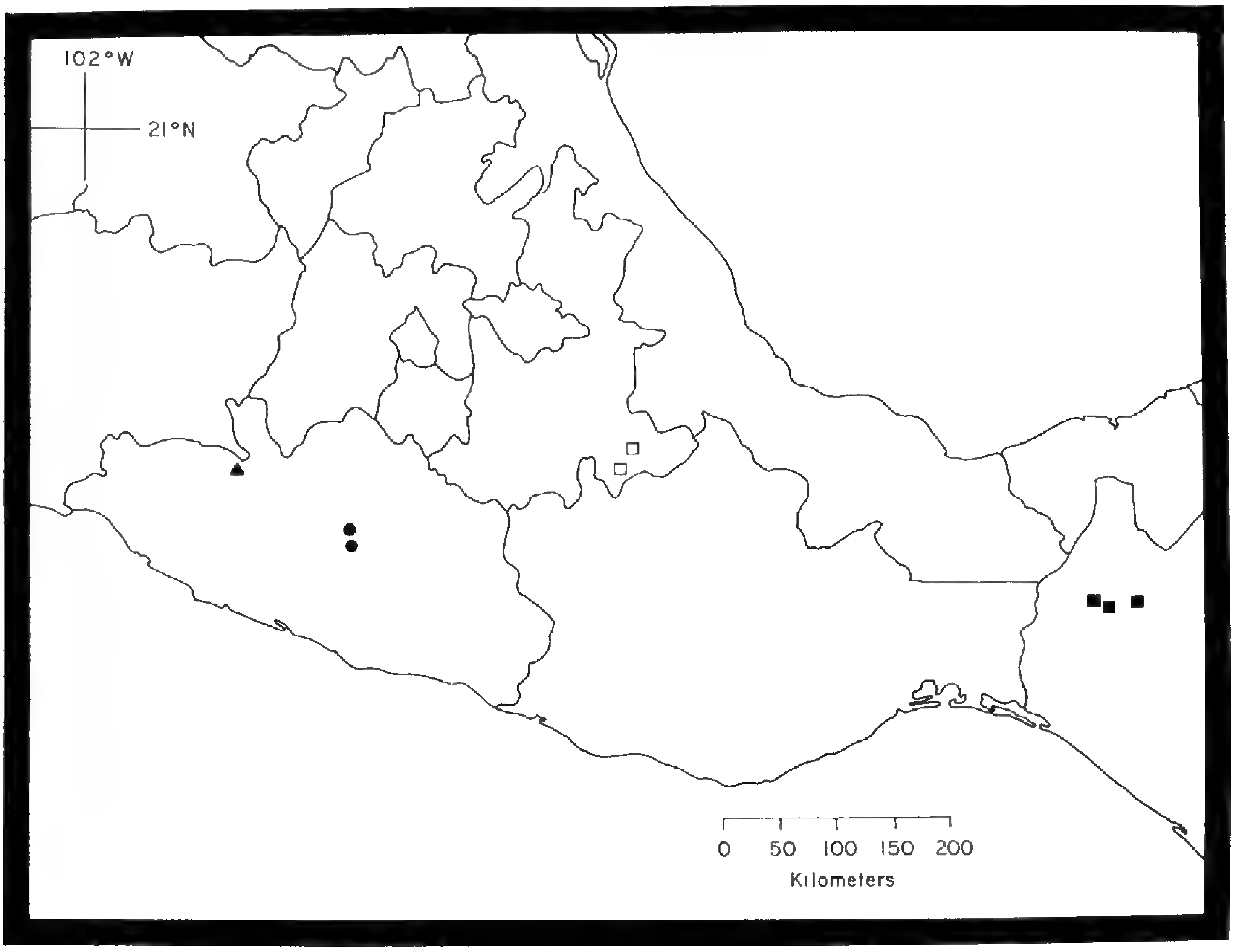
All three collections of this variety from the Cape Region are unusual in their pubescence. The trichomes of the younger stems are scaberulous and 0.05–0.2 mm long, resembling those of *Holographis virgata* subsp. *glandulifera* var. *glandulifera.* The surfaces of the leaves are also scaberulous, but the margin and the veins have the long, flexuose trichomes characteristic of *H. virgata* subsp. *glandulifera* var. *palmeri.*

Although some duplicates of *A. Carter & Ferris 3819* from the Sierra de la Giganta contain both *Holographis virgata* subsp. *glandulifera* var. *glandulifera* and *H. virgata* subsp. *glandulifera* var. *palmeri,* Ms Carter notes (pers. comm.) that the material of the latter variety was collected at about 688 m. Material of the former variety (*A. Carter & Ferris 3829a*) was collected on the same day at about 584 m. It is not known if some of these collections were inadvertently mixed or if the two varieties indeed grow together. The difference in elevation between these two collections is not great.

3. **Holographis argyrea** (Leonard) T. F. Daniel, comb. nov.

Lundellia argyrea Leonard, Wrightia **2:** 1. 1959. TYPE: Mexico, Guerrero, cliff along stream near Chilpancingo, km 276, 21 Oct. 1943, *Lundell 12603* (holotype, US!; isotypes, LL, MICH!).

Erect, rounded shrub to 1 m tall. Older stems splitting in several lines, giving rise to numerous pronounced channels, glabrate; younger stems purplish, epi-



MAP 3. Southern Mexico, showing distribution of *Holographis argyrea* (solid dots), *H. hintonii* (solid triangle), *H. parayana* (solid squares), and *H. pueblensis* (open squares).

dermis soon becoming silvery white, quadrate to ellipsoid in cross section, the surface fluted, evenly pubescent, with trichomes often very sparse, eglandular, retrorse, 0.05 mm long or less. Leaves opposite, ascendant to horizontal; petiole to 10 mm long, pubescent like stems; lamina ovate to orbicular (to obovate), rounded to acute (to subattenuate) at base, rounded to acute at apex, 12–64 by 10–35 mm, 0.9 to 2.2 times longer than wide, the margin entire, flat to subrevolute, ciliate with erect to flexuose trichomes 0.05–0.6 mm long, especially near base, the surfaces sparsely pubescent or subglabrous (surfaces of unfolding leaves densely tomentose with dendroid trichomes), abaxial surface punctate. Inflorescences densely bracteate, terminal spikes to 4.5 cm long; axes pubescent with mixture of glandular and eglandular trichomes, the former 0.2–0.5 mm long, the latter erect, 0.1–0.3 mm long; flowers opposite at spike nodes; bracts lanceolate, 5.5–7 by 2–2.5 mm, pubescent like inflorescence axis; bractlets lance-subulate, approximately same length as subtending bract, 5–6.5 by 0.7–1.2 mm, pubescent like bracts. Calyx 6.5–7.5 mm long, the lobes lance-subulate, pubescent like bracts; corolla yellow with maroon markings, vertical at anthesis, 7–9.5 mm long, pubescent on outer surface with eglandular trichomes, the tube 5–5.5 mm long, slightly ampliate, the upper lip 1–2.5 mm long, with lobes 0.5–1.5 mm long, the lower lip 3.5–4 mm long, with lobes spatulate, 2.5–3.5 by 1.5–3.5 mm; stamens 1.5 mm long, the filaments 0.5 mm long, pubescent, the thecae 1–1.3 mm long, pubescent; staminode 0.2–0.3 mm long, glabrous; ovary glabrous, the style 4 mm long, glabrous, flared at apex, the stigma unequally bilobed, with longer lobe to 0.5 mm long. Capsules not seen.

DISTRIBUTION AND HABITAT. Known only from semiarid Río Balsas basin in central Guerrero (MAP 3); rocky cliffs in low, deciduous thorn forest ca. 700 m alt.; with columnar cacti.

FLOWERING AND FRUITING. Collected only during late October, but undoubtedly flowering well into November; fruiting apparently several weeks after flowering.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** GUERRERO: Cañón de Zopilote, along road to Filo de Caballo, 0.6 mi W of jct. Hwy. 95, *T. Daniel 1193* (ASU, ENCB, GH, MICH), *1242* (CAS, DUKE, MEXU, MICH).

Leonard (1959, p. 1) noted a relationship of *Holographis argyrea* with *Aphelandra.* He believed the genus *Lundellia* could be distinguished from *Aphelandra* by its corky, fissured stems, its oval, silvery laminas, its dendroid hairs, and its "compact solitary terminal glandular spikes of small yellow flowers with their deeply included, almost sessile stamens. . . ." Although *H. argyrea* would be an anomaly in *Aphelandra,* none of these features distinguish it from *Holographis.* Its closest relative appears to be *H. virgata*; both have opposite leaves, silvery stems, and terminal spikes.

4. **Holographis ilicifolia** Brandegee, Zoe **5:** 236. 1906. TYPE: Mexico, Coahuila, Peña (25°28′N, 102°34′W), Feb. 1905, *Purpus 1327* (holotype, UC!; isotypes, GH!, MO!, NY!). FIGURE 3.

Twiggy, erect to spreading, often rounded subshrub to 3(–5) dm tall, arising from stout or tortuous woody base to 10 mm in diameter. Older stems woody, pubescent or glabrate; younger stems green, terete in cross section, the surface smooth to striate, evenly and densely pubescent, often making the stems appear pallid, the trichomes eglandular, retrorse to erect, 0.05–0.2 mm long. Leaves whorled, ascendant or decurved, sessile to subsessile; petiole (if present) 0.1–0.5 mm long, pubescent; lamina coriaceous, orbicular, usually partially folded lengthwise along midvein, cuneate to truncate to subcordate at base, acute-aristate at apex with spine to 3 mm long, (1.5–)3–10 by 2.8–10 mm, 0.8 to 1.3 times longer than wide, the margin spinose toothed, with spines remote, 3 to 6 per side, 0.1–1.5 mm long, the surfaces sparsely pubescent, with trichomes erect to retrorse, 0.01–0.2 mm long. Inflorescences axillary spikes to 4 cm long; axes pubescent like younger stems; flowers alternate along spike axis; bracts ovate to triangular to subulate, (1–)1.5–3 by 0.6–1 mm, pubescent like inflorescence axis; bractlets subulate, longer than subtending bract, (2–)2.5–4 by 0.6–1 mm. Calyx 5–8 mm long, lobes linear-subulate, outer surface pubescent like inflorescence axis, margin densely ciliate with flexuose, eglandular trichomes to 0.3 mm long and glandular trichomes to 0.05 mm long; corolla yellow, usually with dull maroon markings on outer surface, 10–14 mm long, pubescent on outer surface with eglandular trichomes, the tube 5–7 mm long, ampliate above, the upper lip 4–5.5 mm long, with lobes 1–3 mm long; the lower lip 5–7.5 mm long, with lobes spatulate, 4–5.5 by 2.5–4 mm; stamens 4.5–6 mm long, the filaments 3.5–4.5 mm long, more or less densely pubescent

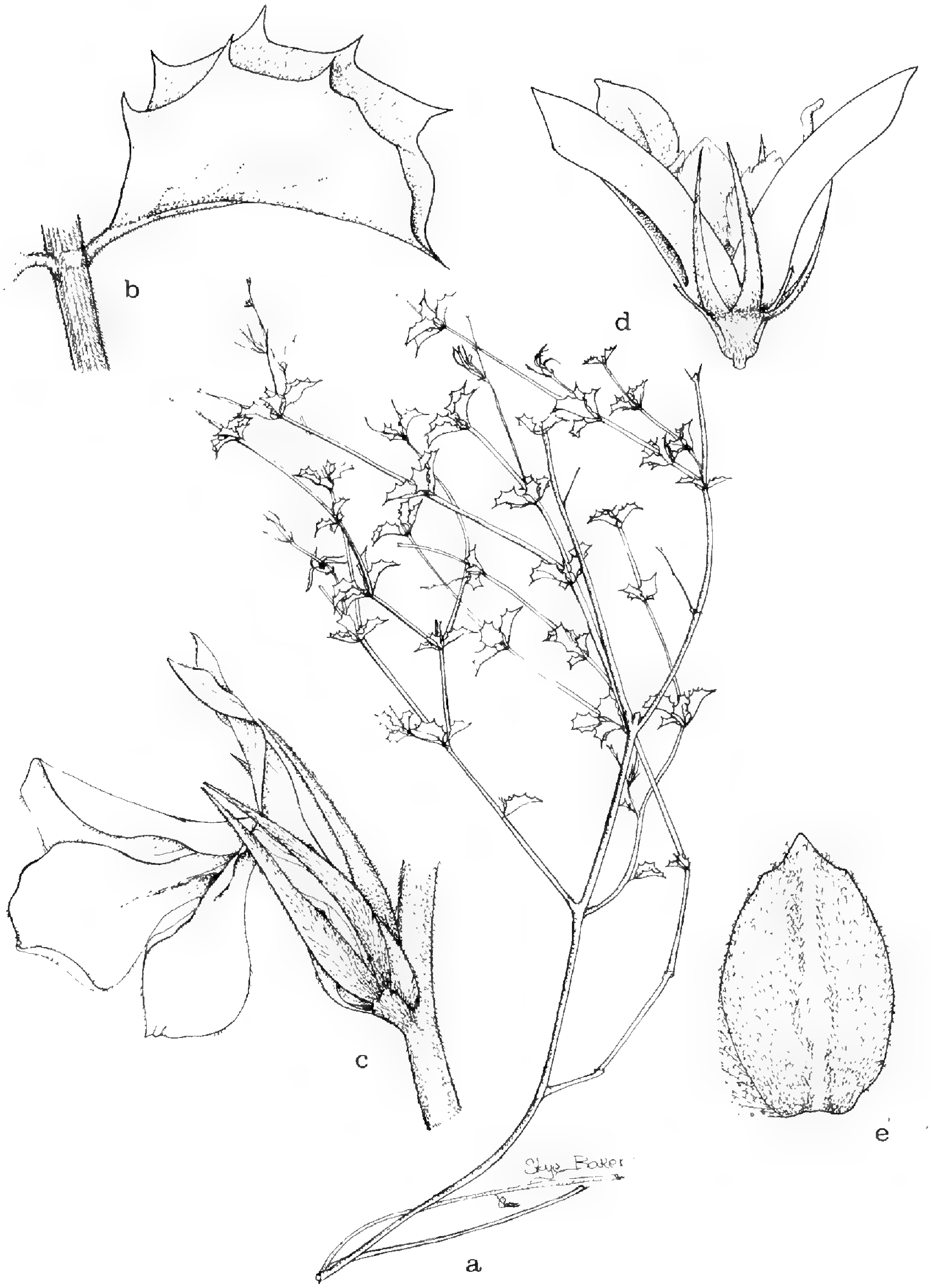


FIGURE 3. *Holographis ilicifolia:* a, habit (*T. Daniel 659*), × 0.6; b, leaf (*T. Daniel 674*), × 7; c, flower (*T. Daniel 674*), × 3.5; d, capsule (*Correll & I. Johnston 21435*), × 3.8; e, seed (*Correll & I. Johnston 21435*), × 10.5.

with trichomes to 0.3 mm long, the thecae 1.2–1.5 mm long, pubescent along dorsal side; staminode 0.5–0.9 mm long, pubescent at base if at all; style 6–8.5 mm long, glabrous, flared at apex, the stigma lobes indistinct. Capsules brown, ellipsoid, 8–10 mm long, 2–3.5 mm in diameter, glabrous or pubescent, trichomes to 0.1 mm long (rarely restricted to apex); retinacula 1–1.5 mm long. Seeds oval, asymmetric at base, 2.5–3.5 by 1.5–3 mm, densely pubescent with dendroid trichomes to 0.5 mm long.

DISTRIBUTION AND HABITAT. Central and southwestern Coahuila and adjacent regions of northern Durango (MAP 1); on rocky slopes and ridges and in gravelly washes of desert scrub zone, 850–1600 m alt.; with species of *Larrea* Cav., *Agave, Viguiera, Yucca* L., *Fouquieria, Acacia, Hechtia, Mortonia* A. Gray, *Colubrina, Randia* L., *Parthenium* L., *Dasylirion* Zucc., *Leucophyllum* Humb. & Bonpl., *Jatropha, Mimosa,* and *Opuntia.*

FLOWERING AND FRUITING. Flowering February through September; fruiting during same period.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** COAHUILA: Puerto de Ventanillas along Hwy. 30 N of San Pedro, 7.1 mi SW of turnoff to Delicias, *T. Daniel 659* (ASU, GH, MEXU, MICH, TEX, US); Valle de San Lucas in Sierra del Venado, N of El Mezquite, 7.5 mi W of Hwy. 30, *T. Daniel 674* (DUKE, ENCB, MICH); ca. 23 mi NW of Las Delicias in valley N of Sierra de las Delicias, *Henrickson 6110* (ASU); ca. 32 mi NE of Tlahualilo in NW portion of Sierra de las Delicias, *Henrickson 12217* (MICH); ca. 72 mi SW of Cuatro Ciénegas on E side of Sierra de las Delicias, 1.5 mi SW of Las Delicias, *Henrickson 12257* (MICH); ca. 67 mi SW of Cuatro Ciénegas, 1.5 mi SW of Las Delicias, *Henrickson 12466* (ASU); vic. of Aguaje del Pajarito, 2–3 km N of Puerto Colorado, *I. Johnston 8675* (F, GH, LL); NE edge of Cerro Bolas, 10.7 km SW of El Solon on Rte. 40, *M. Johnston et al. 8282* (LL); 12.6 km NNE of Las Margaritas in canyon in E face of Sierra de las Margaritas, *M. Johnston et al. 9504b* (LL), *9517* (LL), *10362A* (LL); Cañón de Fora, ca. 35 km W of Cuatro Ciénegas, *M. Johnston 10910* (LL); S part of Sierra de los Organos, 9.5 km E of Puerto del Gallo, *M. Johnston et al. 12137* (LL); ca. 7 mi W of Cuatro Ciénegas, *M. Powell et al. 2286* (TEX, WIS); Cañón de la Fora, ca. 1.1 mi by road E of Est. Socorro, *Wendt & Lott 1199* (LL); 22 mi W of Cuatro Ciénegas, *White 1949* (ARIZ, GH, MEXU, MICH). DURANGO: 7 mi SE of Conejos, *Correll & I. Johnston 21435* (LL, US).

Brandegee (1906) was somewhat doubtful of the generic position of this species when he described it based on Purpus's collection from southwestern Coahuila. He stated (p. 237), "This plant is not strictly congeneric with the little known genus *Holographis,* but it seems best to place it there." Standley did not see any specimens of *H. ilicifolia* and did not include a description of it in his treatment of the Acanthaceae of Mexico (1926).

Now known rather extensively from the Chihuahuan Desert region, this species is the most unusual in the genus. It is unique among the known species of *Holographis* in its spinose-toothed, conduplicate leaves and its alternate arrangement of flowers along the spikes. In addition, the orientation of the corolla is somewhat intermediate between vertical and horizontal, and the staminode arises from the corolla up to 2 mm beyond the filaments of the fertile stamens. Although the generic position of this apparently highly specialized species is no longer in doubt, its closest relatives are not obvious.

5. **Holographis parayana** Miranda, Anales Inst. Biol. Univ. Nac. México **24:** 94. 1953. TYPE: Mexico, Chiapas, arriba La Chacona, cerca de la carretera a San Fernando, unos 10 km NO de Tuxtla Gutiérrez, 7 Jan. 1951, *Miranda 6812* (holotype, MEXU!; isotype, F!).

Erect shrub to 2.5 m tall. Older stems pubescent or glabrate; younger stems greenish to purplish, terete to subquadrate in cross section, the surface striate, evenly pubescent, with trichomes ascendant-appressed, 0.1–0.3 mm long. Leaves whorled, ascendant to horizontal; petiole to 4 mm long, pubescent; lamina lance-ovate to ovate, attenuate to acute to truncate at base, acute at apex, 7–50 by 3.5–15 mm, 1.5 to 3.3 times longer than wide, the margin entire, flat, ciliate, the surfaces pubescent, abaxial surface often more densely so. Inflorescences axillary spikes to 1 cm long; axes pubescent with eglandular, ascendant to flexuose trichomes 0.05–0.3 mm long, occasionally also with glandular trichomes to 0.1 mm long; flowers opposite at spike nodes; bracts triangular to lance-subulate, 2–2.8 by 0.9–1.2 mm, pubescent like inflorescence axis; bractlets triangular to lance-subulate, shorter than subtending bract, 1.5–2 by 0.8–1 mm, pubescent like bracts. Calyx 2–3 mm long, the lobes lance-subulate, pubescent like bracts; corolla pinkish (label data), horizontal at anthesis, 9–10 mm long, pubescent on outer surface with mixture of glandular and eglandular trichomes, the tube 3.5–4 mm long, ampliate above, the upper lip 3–3.5 mm long, with lobes 1–1.5 mm long, the lower lip 4.8–6 mm long, with lobes spatulate, 3–3.5 by 1–2 mm; stamens 3 mm long, the filaments 2 mm long, sparsely pubescent, anterior pair often more densely so, the thecae 1.2–1.5 mm long, very sparsely pubescent; staminode 1 mm long, pubescent at apex; ovary glabrous, the style 5–6 mm long, glabrous, not conspicuously flared at apex, the stigma unequally bilobed, longer lobe to 0.5 mm long. Capsules 12–13.5 mm long, 5 mm in diameter, glabrous; retinacula 3 mm long. Seeds nearly circular in outline, 2.5 mm in diameter, pubescent with dendroid trichomes 0.1–0.3 mm long.

DISTRIBUTION AND HABITAT. Known only from vicinity of Tuxtla Gutiérrez, west-central Chiapas (MAP 3); low deciduous forests at ca. 900 m alt.

FLOWERING AND FRUITING. Flowering in January; fruiting in June.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: cerca y arriba Piñitas, NE Tuxtla G., *Enriquez 6851* (MEXU); arriba Encañada, NO Tuxtla G., *Miranda 5874* (MEXU); arriba Chacona–San Fernando, NO Tuxtla G., *Miranda 6827* (US); Chacona, *Miranda 7209* (MEXU).

Miranda (1953) noted the relationship between this species and *Holographis ehrenbergiana.* He claimed that the two could be distinguished by the flat and larger leaves, the smaller flowers, and the strongly curved corolla tube of *H. parayana.* Comparison of numerous characters in all of the species of *Holographis* indicates that the affinities of *H. parayana* are probably with *H. hintonii* and *H. anisophylla,* with which it shares numerous features including a relatively short, glandular corolla.

6. **Holographis anisophylla** T. F. Daniel, sp. nov. FIGURE 4.

Frutex erectus. Caules juniores pubescentes trichomatibus eglandulosis 0.05–0.1 mm longis. Folia verticillata, in quoque nodo quatuor; laminae lanceolatae vel lanci-ovatae, 9–27 mm longae, 2–8 mm latae, 2.2–4.5-plo longiores quam latiores, marginibus planis ciliatis. Inflorescentia spicata; bracteae lanci-ovatae

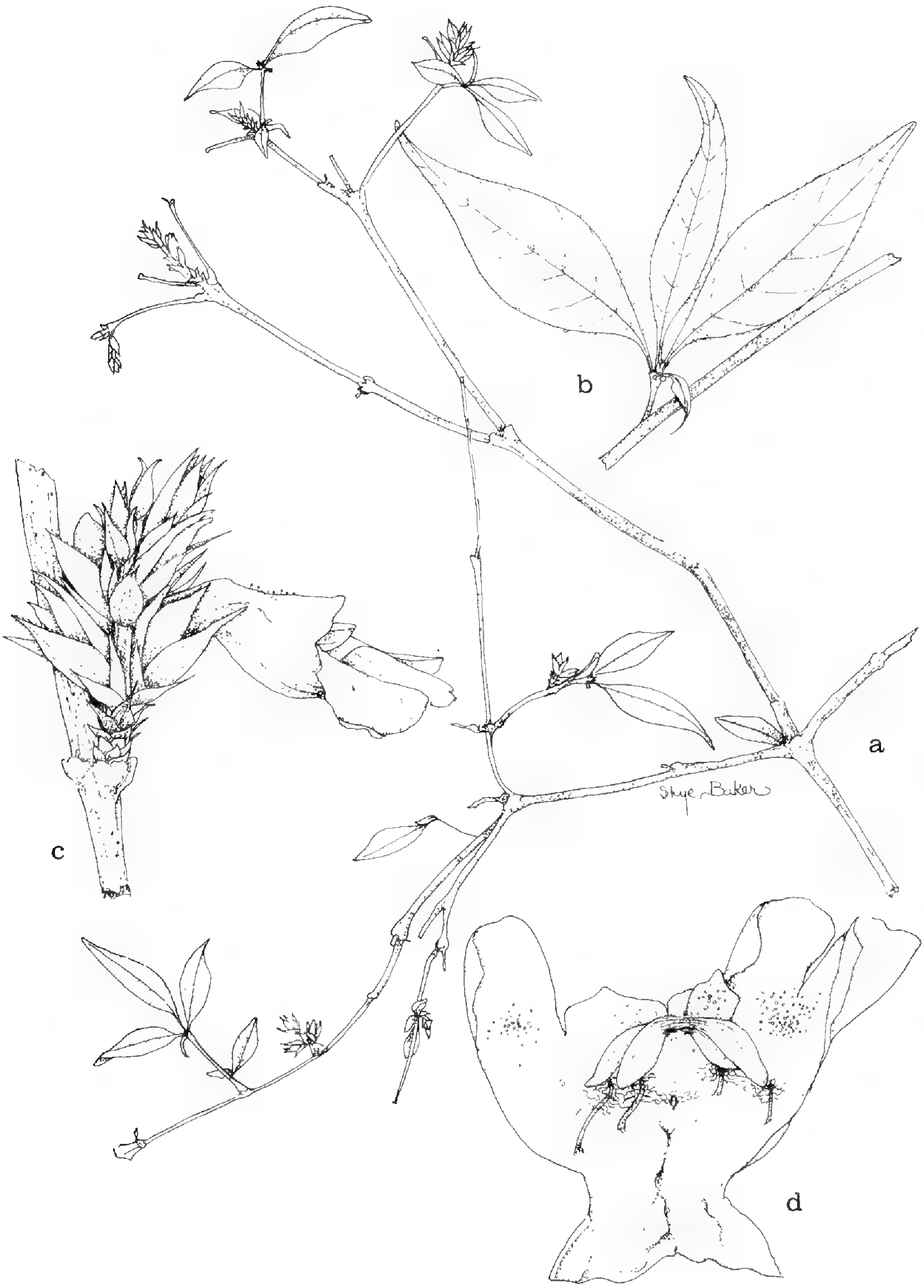


FIGURE 4. *Holographis anisophylla* (from holotype): a, habit, × 0.7; b, node with leaves, × 1.4; c, spike with mature flower, × 3.8; d, dissected flower, × 5.

vel ovatae, 2.5–3 mm longae, 1–2 mm latae; bracteolae lanci-ovatae vel ovatae, 2–2.8 mm longae; calyx 4.5–5 mm longus; corolla 8–9 mm longa, utrinque glandulosa; stamina 2.5–3 mm longa filamentis 1.3–1.6 mm longis; staminodium 0.3 mm longum, apice pubescens; stylus 3.5 mm longus glaber, ovarium basi glabrum, apice pubescens. Capsula ignota.

Erect shrub. Older stems glabrate; younger stems purplish turning white, terete in cross section, the surface striate, pubescent with eglandular, retrorse trichomes 0.05–0.1 mm long, trichomes more or less evenly distributed or in 2 vertical lines. Leaves whorled, horizontal to ascendant, sessile to subsessile; petiole, if present, to 1 mm long; lamina lanceolate to lance-ovate, long-attenuate at base, acute to acuminate (to falcate) at apex, 9–27 by 2–8 mm, 2.2 to 4.5 times longer than wide, the 4 leaves at each node unequal in size, with leaves subtending inflorescences considerably reduced, the margin entire, flat, ciliate with ascendant trichomes to 0.5 mm long, the surfaces pubescent. Inflorescences axillary spikes to 17 mm long; axes pubescent with mixture of glandular and eglandular trichomes, the former 0.05 mm long, the latter erect, 0.05–0.1 mm long; flowers opposite at spike nodes; lower bracts (up to 7 series) sterile, triangular, 1–2 mm long; upper bracts fertile, lance-ovate to ovate, 2.5–3 by 1–2 mm, mucronate at apex, pubescent like inflorescence axis, margin lanate with trichomes to 0.5 mm long; bractlets lance-ovate to ovate, approximately same length as subtending bract or slightly shorter, 2–2.8 by 1 mm, mucronate at apex. Calyx 4.5–5 mm long, the lobes lanceolate, mucronate at apex, pubescent like bracts; corolla horizontal at anthesis, color unknown, 8–9 mm long, pubescent on outer surface with mixture of glandular and eglandular trichomes, the tube 4–5 mm long, ampliate above, the upper lip 1.5–2 mm long, with lobes 1 mm long, the lower lip 4 mm long, with lobes obovate, 2.5 by 2.5–2.8 mm; stamens 2.5–3 mm long, the filaments 1.3–1.6 mm long, pubescent with flexuose trichomes to 0.8 mm long, the thecae 1.8–2 mm long, connivent at pubescent apex; staminode 0.3 mm long, pubescent at apex; ovary glabrous below, pubescent with eglandular trichomes at apex, the style 3.5 mm long, glabrous, the stigma lobes equal, 0.4 mm long. Capsules not seen.

TYPE. Mexico, Colima, Desviación cerca Río Salado, 4 Dec. 1959, *Miranda 9052* (holotype, MEXU!).

Holographis anisophylla is known only from the type, a flowering collection from east-central Colima (MAP 1), which was collected in tropical deciduous forest (McVaugh, pers. comm.). It is unique among the known species of *Holographis* in having glands on the inner, as well as the outer, surface of the corolla. It appears to be most closely related to *H. pallida,* a species that occurs approximately 800 km to the northwest of the type locality. Miranda's collection was, in fact, originally identified as the latter species. These two species resemble each other in the form of the cauline trichomes and in the shape of the leaves and bracts; in addition, the whorled leaves of *H. pallida* are frequently anisophyllous. The species can be distinguished from each other by the characters in the following couplet:

1. Bracts 3–5 mm long; bractlets lance-subulate, 3–4 mm long; calyx 5–7 mm long; corolla 10–12 mm long, eglandular; stamens 3.5–4 mm long. .... *H. pallida.*
1. Bracts 2.5–3 mm long; bractlets lance-ovate to ovate, 2–2.8 mm long; calyx 4.5–5 mm long; corolla 8–9 mm long, glandular; stamens 2.5–3 mm long. .... *H. anisophylla.*

7. **Holographis hintonii** (Leonard) T. F. Daniel, comb. nov.

Berginia hintonii Leonard, Kew Bull. **1938:** 64. 1938. TYPE: Mexico, Guerrero, District of Coyuca, between Coyuca de Catlán and Chamerito, 26 April 1934, *Hinton et al. 5956* (holotype, K!).

Erect shrub. Older stems covered with conspicuous lenticels, glabrous; younger stems subquadrate in cross section, the surface striate-fluted, sparsely pubescent in 2 vertical lines, with trichomes inconspicuous, eglandular, retrorse, 0.05–0.1 mm long. Leaves whorled; petiole up to 8 mm (or more?) long, pubescent with erect to flexuose trichomes to 0.2 mm long; lamina apparently ovate-elliptic (see discussion), attenuate at base, to about 45 (or more?) by 20 (or more?) mm, the margin entire, flat, ciliate, the surfaces sparsely pubescent with flexuose trichomes to 0.8 mm long, the veins on the lower surface densely pubescent. Inflorescences congested axillary spikes to 10 mm (or more?) long; axes obscured by dense mats of crooked, interwoven trichomes to 0.8 mm long (villous); flowers opposite at spike nodes; lower bracts (up to 4 series) sterile, triangular, smaller than upper bracts; upper bracts fertile, broadly ovate to orbicular, 1.5–2 by 1.2–1.5 mm, mucronate at apex, pubescent with mixture of erect glandular and eglandular trichomes to 0.2 mm long, margin villous-ciliate; bractlets lanceolate, approximately same length as subtending bract, 1.5–2 by 0.7–0.9 mm, mucronate at apex, pubescent like bracts. Calyx 4–4.5 mm long, the lobes lanceolate, pubescent like bracts (but glands often more numerous and conspicuous); corolla color unknown, orientation unknown, 8–9.5 mm long, pubescent on outer surface with mixture of eglandular and glandular trichomes, the tube 2–2.5 mm long, the upper lip 3–4 mm long, with lobes 2–3 mm long, the lower lip 6–7 mm long, with lobes orbicular, 3–3.5 mm in diameter; stamens 3–3.5 mm long, the filaments 1–1.5 mm long, densely pubescent with flexuose trichomes to 0.8 mm long, the thecae 2 mm long, sparsely pubescent; staminode 0.4 mm long, glabrous; style 4 mm long, pubescent, the stigma lobes 0.5 mm long. Capsules 10–11 mm long, 3–4 mm in diameter, pubescent, with trichomes eglandular, 0.1–0.2 mm long. Seeds 4 by 2.5 mm, pubescent with dendroid trichomes to 0.3 mm long.

This species is presently known only from the type, which was collected in flower and fruit in late April in the semiarid region of northwestern Guerrero (MAP 3). Although this specimen of *Holographis hintonii* is leafless, the size of the leaf scars and a fragment of the basal portion of a leaf in a packet attached to the specimen indicate relatively large, petiolate, ovate-elliptic leaves, probably similar in form to those found in *H. tamaulipica.*

When he described this species (as *Berginia hintonii*), Leonard (1938) noted that it was distinctive in *Berginia* in having "short bract-covered peduncles and short tomentose spikes." In *Holographis* its closest relatives appear to be *H. parayana* and *H. anisophylla*; all three have entire, flat leaves and relatively small (8–10 mm long), glandular corollas.

8. **Holographis pallida** Leonard & Gentry in Gentry, Brittonia **6:** 324. *fig. 5.* 1948. TYPE: Mexico, Sinaloa, Cerro Llano Redondo, W of Caymanero, 25 April 1944, *H. Gentry 7022* (holotype, MICH!; isotypes, DES!, F!, GH!, NY!, US!).

Erect shrub to 1.3 m tall. Older stems pubescent or glabrate; younger stems gray-green, terete in cross section, the surface smooth to striate, evenly and densely pubescent making the stems appear pallid, the trichomes eglandular, retrorse, 0.05–0.2 mm long. Leaves whorled, ascendant or decurved, subsessile to petiolate; petiole to 5 mm long, pubescent like younger stems; lamina lanceolate to ovate to subelliptic, long-attenuate at base, acute to acuminate (to falcate) at apex, 8–50 by (2–)4–21 mm, 2.5 to 4 times longer than wide, the 4 leaves at a node often unequal in size, the margin entire, flat, ciliate, the surfaces sparsely pubescent, with trichomes often restricted to major veins, abaxial surface somewhat punctate. Inflorescences densely bracted axillary spikes to 3 cm long; axes hirsute, with trichomes erect to recurved, 0.2–0.8 mm long (axes often with inconspicuous, capitate glands to 0.3 mm long as well); flowers opposite at spike nodes; lower bracts (up to 4 series) mostly sterile, triangular, 1–2 mm long; upper bracts fertile, lanceolate to ovate, 3–5 by 1–1.8 mm, mucronate at apex, pubescent like inflorescence axis, with trichomes particularly evident along margin; bractlets lance-subulate, approximately same length as subtending bract, 3–4 by 0.8–1 mm, mucronate at apex. Calyx 5–7 mm long, the lobes lance-subulate, mucronate at apex, pubescent like bracts; corolla "white to pale lavender" (label data), horizontal at anthesis, 10–12 mm long, pubescent on outer surface with eglandular trichomes, the tube 5–6 mm long, ampliate above, the upper lip 2–3 mm long, with lobes 0.8–1.5 mm long, the lower lip 5–6 mm long, with lobes spatulate, 3–5 by 2–4 mm; stamens 3.5–4 mm long, the filaments 1.5–2 mm long, pubescent with flexuose trichomes to 0.4 mm long, the thecae 1.5–2 mm long, pubescent along dorsal side, connivent around style; staminode reduced to minute, glabrous projection 0.1 mm long; style 5.3–6 mm long, glabrous or sparsely pubescent, flared at apex, the stigma equally bilobed, with lobes to 0.5 mm long. Capsules 7–9 mm long, 3 mm in diameter, pubescent on outer surface with eglandular trichomes 0.1–0.2 mm long; retinacula 1.5 mm long. Seeds oval, 2.2 by 1.9 mm, densely pubescent with dendroid trichomes to 0.2 mm long.

DISTRIBUTION AND HABITAT. Southern Sonora and central Sinaloa (MAP 1); in arroyos and on rocky slopes in thorn forest, ca. 50–500 m alt.

FLOWERING AND FRUITING. Flowering in February and April, when leaves appear to begin flushing; fruiting in April.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** SONORA: San Bernardo, *H. Gentry 1350* (A, ARIZ, DES, F, MO, UC), *3615* (ARIZ, F); Sierra Bojihuacame, SE of Cd. Obregón, *H. Gentry 14492* (US).

Leonard and Gentry (*in* Gentry, 1948) noted the apparent uniqueness among American Acanthaceae of the monothecous stamens with connivent anthers in this species and suggested that the plant may be worthy of generic status.

In the present study this character was found to be almost universal among species of *Holographis*. Leonard and Gentry further noted the similarity of this species to members of *Berginia*; indeed, Gentry's label on the type bears a preliminary name in this genus. Finally, they concluded that *Holographis* and *Berginia* were probably congeneric.

The closest relative of *Holographis pallida* appears to be *H. anisophylla*. The similarities between them are discussed under the latter species.

9. **Holographis pueblensis** T. F. Daniel, sp. nov. Figure 5.

Suffrutex vel frutex erectus usque ad 5 dm altus. Caules juniores pubescentes trichomatibus eglandulosis, 0.2–0.8 mm longis. Folia supera verticillata, in quoque nodo quatuor; laminae ovatae vel ellipticae, 5–24 mm longae, 3–15 mm latae, 1.5–2-plo longiores quam latiores, marginibus revolutis ciliatis. Inflorescentia spicata; bracteae anguste lanceolatae vel lanci-subulatae, 6.5–11 mm longae, 1.5–2 mm latae; bracteolae lanci-subulatae, 5.5–9 mm longae. Calyx 7–10.5 mm longus; corolla aurea, 15–18 mm longa, extus pubescens; stamina 9–11 mm longa filamentis 8–8.5 mm longis apicibus glabris basibus pubescentibus; staminodium 0.4–0.5 mm longum pubescens; stylus 12–16 mm longus glaber, ovarium glabrum.

Erect subshrub to shrub to 5 dm tall arising from stout, woody base to 5 mm in diameter. Older stems pubescent or glabrate; younger stems terete in cross section, the surface smooth to striate, evenly (often densely) pubescent, with trichomes eglandular, ascendant-appressed, 0.2–0.8 mm long. Leaves whorled (lower leaves sometimes opposite or subopposite), ascendant to horizontal, subsessile to petiolate; petiole to 8 mm long, pubescent with flexuose to ascendant trichomes to 1 mm long; lamina ovate to elliptic, attenuate to acute to truncate at base, acute to rounded at apex, 5–24 by 3–15 mm, 1.5 to 2 times longer than wide, the margin entire, revolute, ciliate, the surfaces pubescent, the abaxial surface often punctate. Inflorescences axillary, densely bracted spikes to 4.5 cm long; axes pubescent with erect to ascendant trichomes 0.2–0.5 mm long; flowers opposite at spike nodes; bracts narrowly lanceolate to lance-subulate, 6.5–11 by 1.5–2 mm, tapering to point but not mucronate at apex, pubescent like inflorescence axis; bractlets lance-subulate, approximately same length as subtending bract, 5.5–9 by 1–1.8 mm, pubescent like bracts. Calyx 7–10.5 mm long, the lobes lance-subulate, outer surface sparsely pubescent (often glabrous near base), margin lanate; corolla yellow, vertical at anthesis, 15–18 mm long, pubescent on outer surface with eglandular trichomes, the tube 7.5–9 mm long, ampliate above, the upper lip 7–8 mm long, with lobes 0.3–0.5 mm long, the lower lip 7.5–9 mm long, with lobes spatulate, 4.5–6.5 by 2.2–4 mm; stamens 9–11 mm long, the filaments 8–8.5 mm long, glabrous above, pubescent at base, the thecae 2–3 mm long, pubescent; staminode 0.4–0.5 mm long, pubescent; ovary glabrous, the style 12–16 mm long, glabrous, not flared at apex, the stigma lobes inconspicuous. Capsules not seen.

Type. Mexico, Puebla, vicinity of San Luis Tultitlanapa, near Oaxaca, July 1908, *Purpus 3346* (holotype, UC!; isotypes, F!, GH!, MO!, NY!, US!).

FIGURE 5. *Holographis pueblensis:* a, habit (*Purpus s.n.,* June 1907), × 0.6; b, node with leaves (*Purpus 3346*), × 2.5; c, young spike with flowers (*Purpus 3346*), × 2.2; d, gynoecium (*Purpus 3346*), × 3.

Distribution and habitat. Known only from two Purpus collections from semiarid regions of southeastern Puebla (Map 3).

Flowering and fruiting. Flowering June and July; time of fruiting unknown.

Additional specimen examined. **Mexico.** Puebla: Tehuacán, *Purpus s.n.*, June 1907 (uc).

This species appears to be most closely related to *Holographis ehrenbergiana*, which occurs primarily north of the range of *H. pueblensis* (see discussion under *H. ehrenbergiana*).

10. **Holographis ehrenbergiana** Nees in DC. Prodr. **11**: 728. 1847. Type: Mexico, "supra la Haciende de Guadela [?]," *Ehrenberg 1224* (holotype, b, destroyed). Figure 6.

Erect, often rounded subshrub to shrub to 1.3 m tall, arising from stout, often tortuous woody base to 12 mm in diameter. Older stems pubescent or glabrate; younger stems pale green, terete to subquadrate in cross section, the surface smooth to striate, evenly (often densely) pubescent, with trichomes eglandular, erect to ascendant, 0.1–0.7 mm long. Leaves whorled, ascendant to horizontal, subsessile to petiolate; petiole to 8 mm long, pubescent; lamina lanceolate to obovate, attenuate to acute at base, acute to rounded at apex, 5–35 by 2–16 mm, 1.9 to 3.5 times longer than wide, the margin entire, revolute, ciliate, the surfaces pubescent, abaxial surface often more densely so (sometimes becoming lanate). Inflorescences axillary spikes to 2 cm long, usually reduced to 2 flowers; axes pubescent like younger stems; bracts triangular to subulate, 1.5–5 by 0.5–1 mm, emucronate, sparsely to densely pubescent with erect to flexuose trichomes to 1 mm long; bractlets subulate, approximately same length as subtending bract or slightly longer, (1.5–)2.5–5 by 0.5 mm, pubescent like bracts. Calyx 3.5–6 mm long, the lobes lance-subulate, pubescent like bracts; corolla yellow, vertical at anthesis, 12–18 mm long, pubescent on outer surface with eglandular trichomes, the tube 6–10 mm long, ampliate above, the upper lip (6–)7.5–9 mm long, with lobes 0.3–1 mm long, the lower lip (5.5–)8–10 mm long, with lobes spatulate, 4.5–6 by 2–4.5 mm; stamens 9–11 mm long, the filaments 8–10 mm long, glabrous or pubescent at base, the thecae 1.5–2.3 mm long, densely pubescent; staminode 0.5–1.3 mm long, pubescent at base; style 12–14 mm long, sparsely pubescent (some individual styles glabrous, but at least some styles sparsely pubescent on each plant), not flared at apex, the stigma lobes inconspicuous. Capsules 10–15 mm long, 4–4.5 mm in diameter, glabrous; retinacula 2–3 mm long. Seeds suboval, 3.5–4.8 by 2.5–3.5 mm, glabrous.

Distribution and habitat. Central Nuevo León and Tamaulipas south through San Luis Potosí and Hidalgo, apparently to southeastern Puebla (Map 1); rocky limestone slopes at 150–2000 m alt.; in arid and semiarid associations with species of *Mimosa*, *Flourensia* DC., *Acacia*, *Colubrina*, *Agave*, *Neopringlea* S. Watson, *Cordia* L., *Bonetiella* Rzedowski, *Fouquieria*, and *Yucca*.

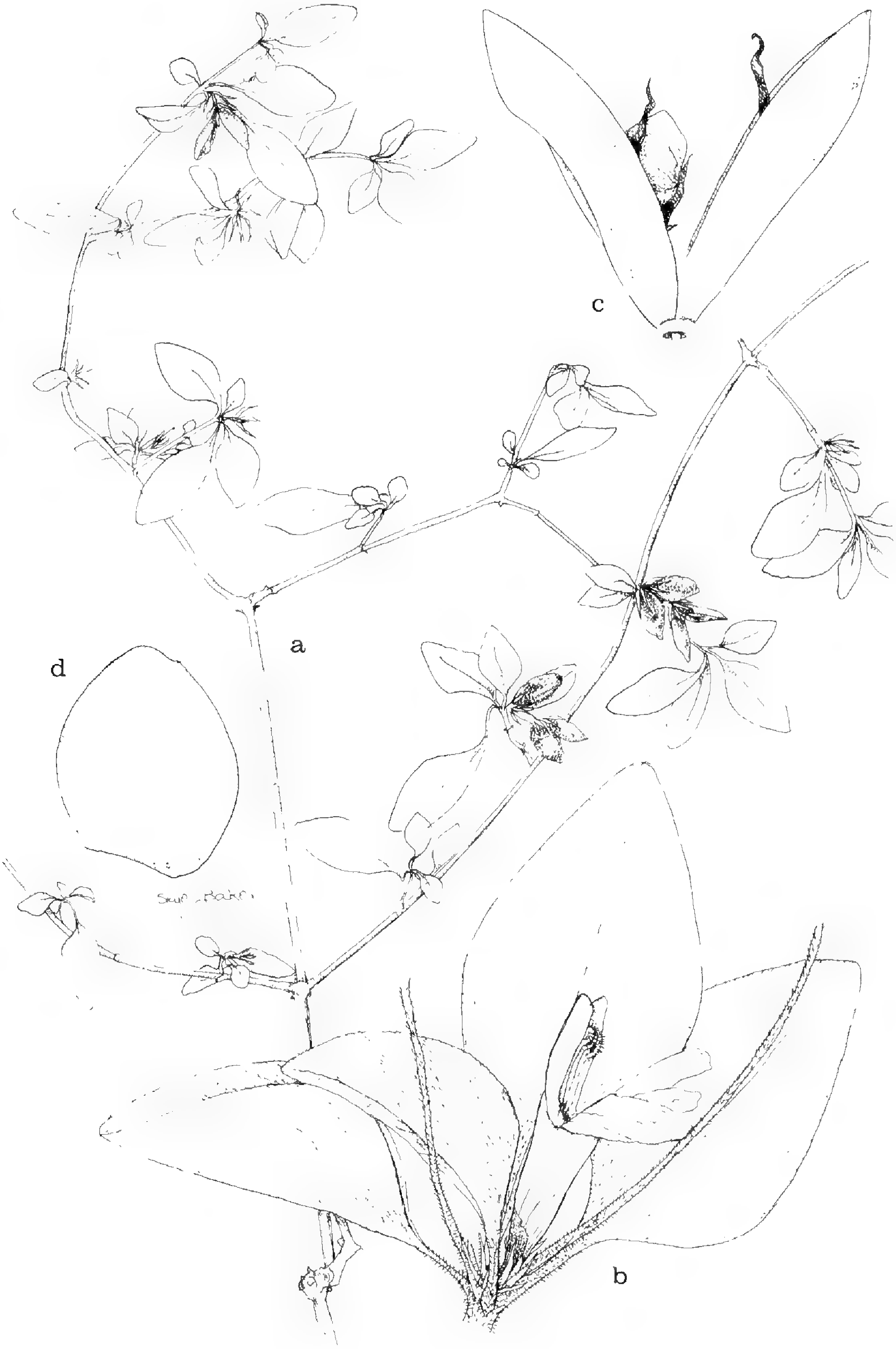


FIGURE 6. *Holographis ehrenbergiana:* a, habit (*Purpus 4921*), × 0.6; b, node with leaves and flower (*Moore & Wood 4406*), × 2; c, capsule (*Purpus 4921a*), × 3.8; d, seed (*Purpus 4921a*), × 6.8.

FLOWERING AND FRUITING. Flowering May through October; fruiting a month or two after flowering.

REPRESENTATIVE SPECIMENS. **Mexico.** HIDALGO: km 147, SE of Ixmiquilpan, *Lundell & Lundell 12342* (LL, MICH); Barranca de Tolimán, above mines on road from Zimapán to Mina Loma del Toro and Balcones, *Moore & Wood 4406* (A, MEXU, MICH, UC, US); Ixmiquilpan, *Purpus 1409* (F, GH, MO, NY, UC); 10 km NW de Zimapán, *González Quintero 3238* (ENCB, MICH); 5 km NW de Actopan, *González Quintero 3581* (DS, ENCB, MICH, MSC). NUEVO LEÓN: Cañón de Huasteca, near Monterrey, near upper spring of Rancho de Ed. Aguirre-Pequeño, *Kruckeberg 4857* (MICH). PUEBLA: Tlacuilotepec, *Purpus 3936* (UC). SAN LUIS POTOSÍ: 20 km E of San Francisco on San Luis Potosí–Río Verde Hwy., 22°00′N, 100°37′W, *M. Johnston et al. 8182* (LL); 10 mi W of Río Verde on road to S.L.P. at microondas station, *M. Johnston et al. 11189* (LL); Río Verde, *Palmer 4* (F, GH, MO, NY, UC, US); Minas de San Rafael, *Purpus 4921* (F, MO, UC, US), *4921A* (GH, MO, UC), *5225* (DES, F, GH, MEXU, MO, NY, UC); E de Núñez, km 48 carretera S.L.P.–Antiguo Morelo, *Rzedowski 5605* (ENCB); ca. 15 km NE de Guadalcázar, *Rzedowski 6031* (ENCB, MEXU, MICH); 40 km S de Matehuala, 6 km E del km 575 de la carretera México–Piedras Negras, *Rzedowski 8254* (ENCB). TAMAULIPAS: Sierra de San Carlos, vic. of San Miguel, *Bartlett 10623* (F, MICH); Cerro El Platero above Rancho El Platero, 0.5 mi S of Ejido El Higuerón (Mpio. Aldama) in Sierra de Tamaulipas, *T. Daniel 268* (MICH); 1 km S of Carabanchel, *Gilbert 74* (TEX); 3 mi E of the San Fernando–Santander Jiménez Hwy. on road to Loreto, *M. Johnston & Crutchfield 5593* (MICH, TEX); by Mex. 85, 10.6 mi N of San José and 16 mi N of Ejido, *Kral 27326* (MO); Buena Vista Hda., *Wooton s.n.,* 14 June 1919 (US). Locality unknown: *Coulter 1211* (GH).

Purpus's specimen from Tlacuilotepec, Puebla, was apparently collected near where *Holographis pueblensis* was growing. Sousa Sánchez (1969) noted that Tlacuilotepec is probably in the region of San Luis Tultitlanapa. It is from this latter locality that the type of *H. pueblensis* was collected. If this locality information is correct, then the range of *H. ehrenbergiana* overlaps those of both *H. tamaulipica* and *H. pueblensis.*

Holographis ehrenbergiana shows considerable variation in the amount of pubescence on the abaxial leaf surface. At one extreme (e.g., *M. Johnston & Crutchfield 5593*) the lower leaf surface is evenly but relatively sparsely pubescent, while in some specimens (e.g., *Moore & Wood 4406*) the trichomes are so dense that the surface is not visible.

Holographis ehrenbergiana appears to be most closely related to *H. pueblensis,* which it superficially resembles. Characters of the inflorescence, bracts, bractlets, and calyx readily distinguish these species, however.

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DEPARTMENT OF BOTANY AND MICROBIOLOGY
ARIZONA STATE UNIVERSITY
TEMPE, ARIZONA 85287

WOOD ANATOMY OF BELLIOLUM (WINTERACEAE) AND A NOTE ON FLOWERING

SHERWIN CARLQUIST

THE GENUS *Belliolum* Van Tieghem occurs in the Solomon Islands and in New Caledonia (Smith, 1943). Of the Solomon Islands species, three were described by Smith (1942); a fourth, *B. haplopus* (Burtt) A. C. Sm., was transferred from *Bubbia* Van Tieghem. Although four New Caledonian species of *Belliolum* were recognized by Van Tieghem (1900), all except *B. pancheri* (Baillon) Van Tieghem are known from inadequate material or are otherwise of uncertain status. This situation will doubtless be remedied by the studies of W. Vink, who has kindly determined my New Caledonian material as *B. pancheri.*

The present study gives comparative data on the wood of *Belliolum,* which has previously been known only from an illustration in Bailey (1944); his article contained a description of the wood of Winteraceae as a whole but no characterization of genera and species. The paucity of material available at that time rendered comparative studies within the family impossible. However, more abundant material now at hand renders comparative studies of winteraceous woods feasible. Patel (1974) produced an admirable monograph of the woods of the genus *Pseudowintera* Dandy, and a study of woods of *Zygogynum* Baillon (Carlquist, 1981) has been published. Comparative study of woods yields not merely taxonomic dividends, but a better understanding of wood in relation to ecology as well.

A few illustrations of flowers of *Belliolum pancheri* and brief descriptions of details of anthesis are appended to supplement the account of pollination of the Winteraceae given by Thien (1980).

MATERIALS AND METHODS

The wood samples of *Belliolum pancheri* analyzed were collected in mid-elevation forests of the Plateau de Dogny, New Caledonia, where the species grows as an understory tree on humid, shady slopes. Wood samples were prepared by removing the bark to facilitate drying. Samples could not be completely dried prior to shipping, so they were enclosed in plastic bags in which paraformaldehyde sufficient to retard fungal growth had been added. Upon receipt in Claremont, these wood samples were extracted, washed, and air dried. This method prevented the mold that would otherwise have grown. The wood sample of *B. pancheri* was 10 cm in diameter.

Wood samples of the Solomon Islands species were provided through the

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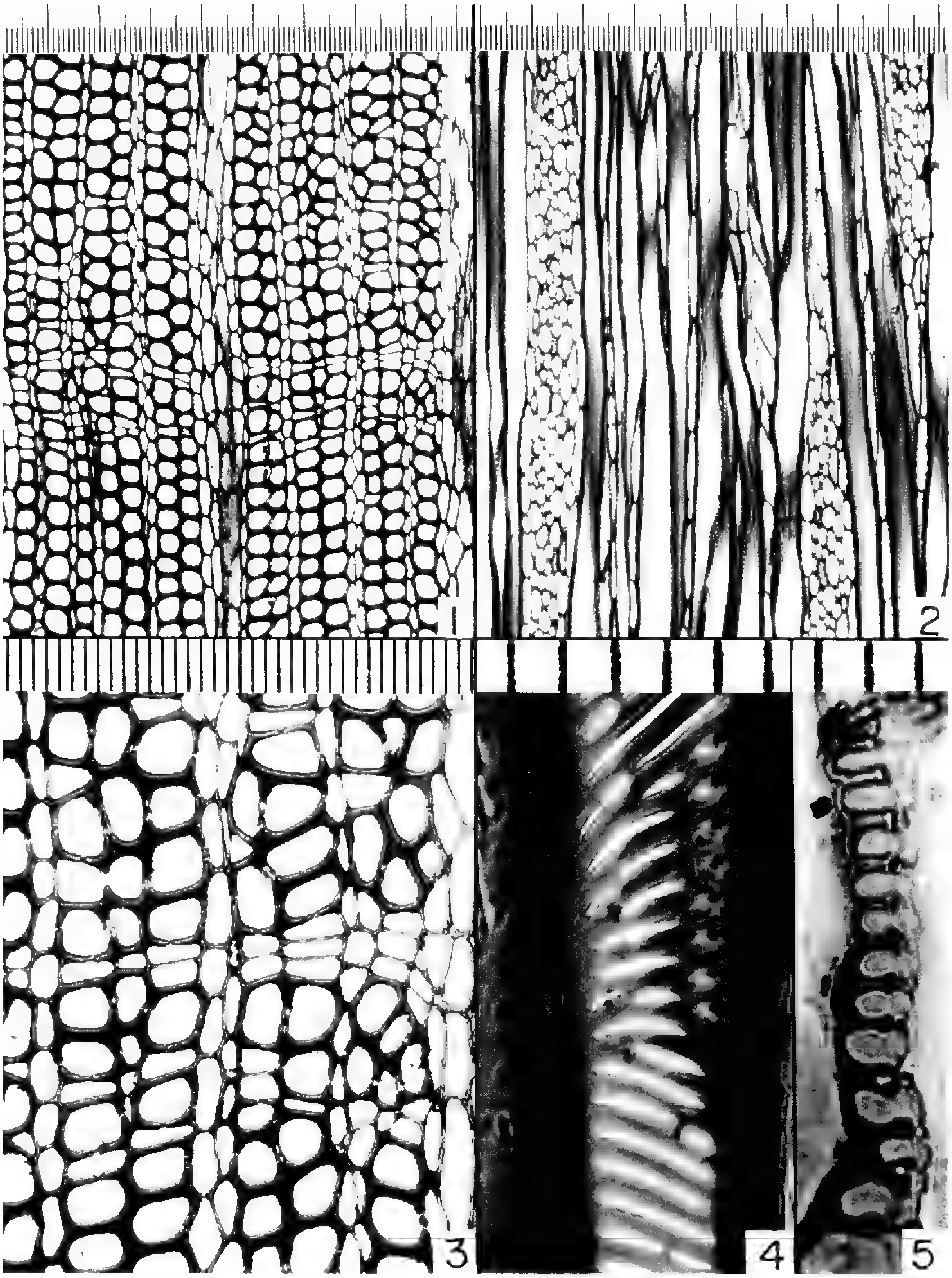


FIGURES 1–5. **Belliolum haplopus** (MADw-22694), wood sections: 1, transverse section, illustrating long and short tangential parenchyma bands; 2, tangential section, showing thin-walled rays; 3, transverse section, tracheids wide and thin walled; 4, radial section, scalariform and transitional pitting on overlap areas of tracheid; 5, radial section, borders of pits on ray-cell walls. Scale: 1, 2, finest divisions = 10 μm; 3–5, divisions = 10 μm.

TABLE 1. **Features of the wood of Belliolum.**

SPECIES AND COLLECTION	TRACHEID DIAMETER (μm)*	TRACHEID WALL THICKNESS (μm)	TRACHEID LENGTH (μm)	RAY WIDTH†
B. gracile, MADw-29483	60	1.4	6290	6.2
B. haplopus, MADw-22694	56	4.8	4902	6.7
B. haplopus, MADw-29285	54	5.4	4570	6.3
B. kajewskii, MADw-29294	50	5.0	3958	6.2
B. pancheri, *Carlquist 15564*	42	7.7	4260	4.4

*Mean diameter at widest point.

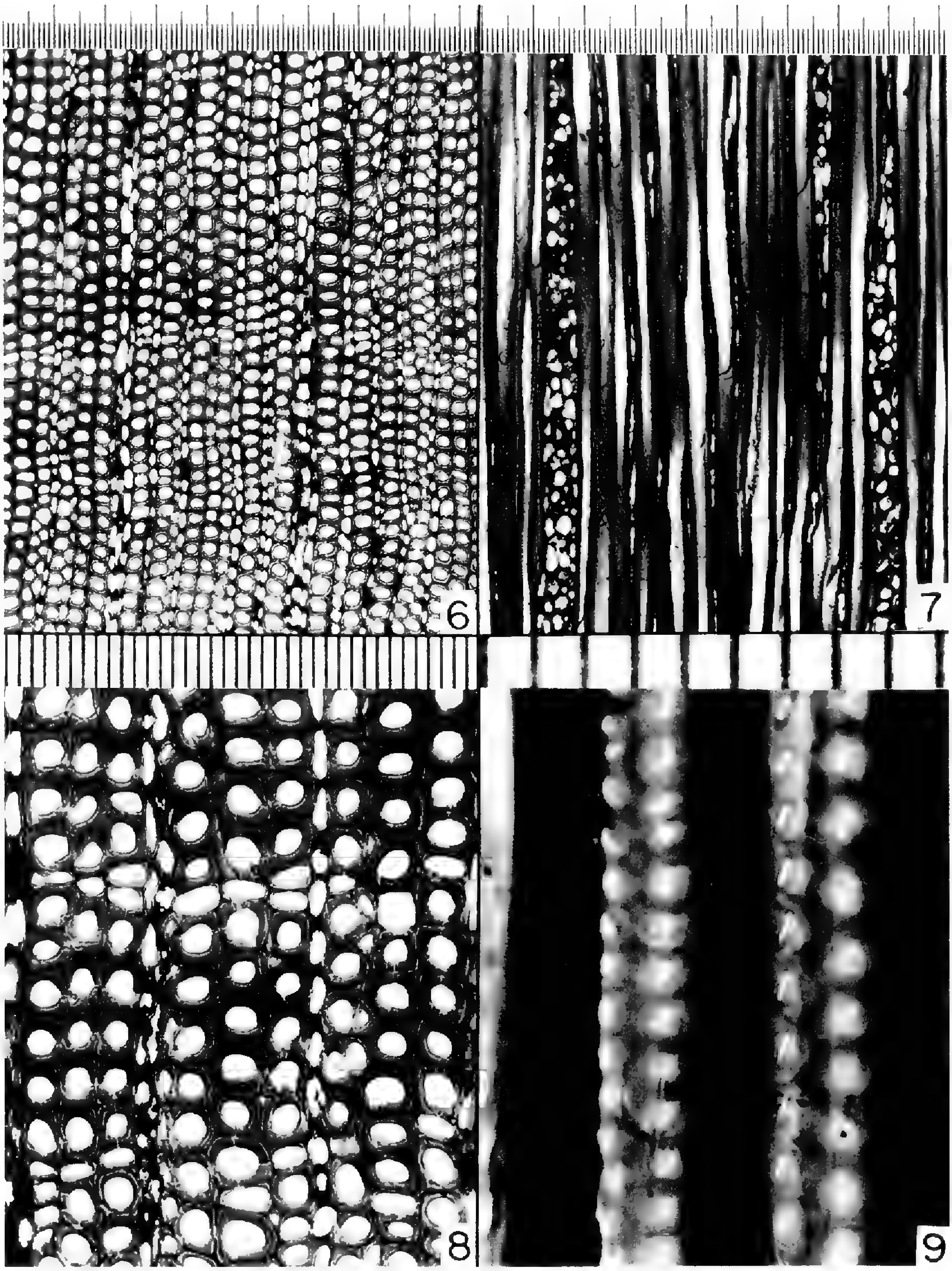
†Number of cells of multiseriate rays at widest point.

kindness of the Forest Products Laboratory of the U. S. Forest Service (MADw). The provenance of these samples is Bougainville Island, as follows: *Belliolum gracile* A. C. Sm., MADw-29483, *R. Schodde & L. Craven 3718* (CANB), primary montane rain forest, 2700 ft (tree 15 m, DBH ca. 20 cm), S foothill slopes of Lake Loloru crater, ca. 17 mi N of Buin; *B. haplopus* (Burtt) A. C. Sm., MADw-22694, no further locality, and MADw-29285, *R. Schodde 261* (CANB), primary rain forest, ca. 2300 ft (small bushy tree ca. 7 m tall, DBH 6 cm), lower S slopes of Lake Loloru crater, ca. 14 mi N of Buin; *B. kajewskii* A. C. Sm., MADw-29294, *L. A. Craven & R. Schodde 307* (CANB), primary montane rain forest with a number of small watercourses, ca. 2200 ft (tree 9 m tall, DBH 12 cm), lower S slopes of Lake Loloru crater, ca. 15 mi N of Buin. The identity of the specimen supplied as *B. gracile* is questionable because that species is not reported by Smith (1942) to occur on Bougainville Island, the provenance of the sample.

The wood sample of *Belliolum pancheri* was boiled and softened with ethylene diamine before being sectioned on a sliding microtome, according to the technique of Kukachka (1977). The wood of *B. pancheri* is moderately hard for a winteraceous wood. Woods of the Solomon Islands species, however, proved too soft for sectioning on a sliding microtome after being boiled (but without any treatment with ethylene diamine). Consequently, an alternative method was used for these species. They were treated with ethylene diamine according to Kukachka's method—but for one month. The woods were then washed, put through a tertiary butyl alcohol series (Johansen, 1940), embedded in paraffin, and sectioned at 15 mm. This novel use of ethylene diamine as a softening agent prior to paraffin sectioning yielded excellent results (see FIGURES 1–5) and is strongly recommended for woods that are extremely soft. All wood sections of *Belliolum* were stained with safranin, while macerations were prepared with Jeffrey's fluid and also stained with safranin.

ANATOMICAL DESCRIPTIONS

As shown in TABLE 1, quantitative data for the *Belliolum* collections were obtained on a limited number of wood features. The figures show that the



FIGURES 6–9. **Belliolum pancheri** (*Carlquist 15564,* RSA), wood sections: 6, transverse section, showing bands of axial parenchyma; 7, tangential section, illustrating narrowness of rays and accumulation of resinlike materials; 8, transverse section, showing thickness of tracheid walls and bands of axial parenchyma; 9, radial section, showing biseriate pits of overlap areas of tracheids. Scale: 6, 7, finest divisions = 10 μm; 8, 9, divisions = 10 μm.

tracheids of *B. gracile* are thinner walled than those of other species. Compared to *B. pancheri* (FIGURE 8), the Solomon Islands species as a whole (e.g., *B. haplopus*, FIGURE 3) have much wider tracheids with thinner walls.

Overlap areas (end walls) of tracheids in some Winteraceae show patterns markedly different from those on lateral walls. Pitting is generally denser on end walls than on lateral walls, and in *Belliolum* can frequently be biseriate (as shown for *B. pancheri* in FIGURE 9) or triseriate. In addition, overlap areas of tracheids in all *Belliolum* species except *B. kajewskii* (which has only the biseriate and triseriate end-wall pitting mentioned above) also bear scalariform, scalariform transitional to opposite, and opposite pitting. The scalariform and scalariform transitional to opposite end-wall pitting types are shown here for *B. haplopus* (FIGURE 4).

Pits on lateral walls of tracheids of *Belliolum* are circular, about 7 μm in diameter, and with elliptic apertures like those of the pits shown in FIGURE 9. Patel (1974) has reported similar pits on *Pseudowintera* tracheids.

The helical thickenings and trabeculae reported by Patel (1974) for tracheids of *Pseudowintera* are not present in *Belliolum*. In groups with characteristics that reflect mesic environmental conditions, helical thickenings may relate to adaptation to areas where frost occurs. This tendency can be traced in such families as Illiciaceae, where such thickenings occur in vessel elements.

Axial parenchyma expressions vary within *Belliolum*. In *B. pancheri* short bands, usually a single cell thick, can be seen in addition to isolated diffuse cells (FIGURE 8). In *B. haplopus* bands are one to three cells thick, but diffuse cells are also present (FIGURE 3). In *B. gracile* and *B. kajewskii*, however, only diffuse cells, occasionally grouped two or three together, were observed. Although the range of axial parenchyma types is somewhat greater in *Zygogynum* (axial parenchyma is scarce in some collections of *Zygogynum*), the two genera are very similar. *Pseudowintera* also has the same range of axial parenchyma types as is found in *Belliolum* (Patel, 1974). Axial parenchyma strands are long in *Belliolum*, commonly ranging from 17 to 24 cells.

Rays vary relatively little in width in *Belliolum* (TABLE 1) but are appreciably narrower in *B. pancheri* (FIGURE 7) than in the Solomon Islands species such as *B. haplopus* (FIGURE 2). This cannot be related to stem size, for the stems of *B. pancheri* are comparable in size to those of *B. gracile* and *B. haplopus*. As judged from Patel's (1974) data, the rays are much narrower in *Belliolum* than in *Pseudowintera*, but are about the same as those in *Zygogynum*.

Ray cells have thicker walls in *Belliolum pancheri* than in the Solomon Islands species. In no species of *Belliolum* did rays contain the ethereal oil idioblasts or sclereids found in some species of *Zygogynum* (Carlquist, 1981). Ray cells, as in *Zygogynum* and *Pseudowintera* (Patel, 1974), often have borders (FIGURE 5). In none of the *Belliolum* species, however, are borders present in all ray cells. Resinlike deposits (FIGURE 5) could be observed in ray cells in all *Belliolum* species but are much more conspicuous in *B. pancheri* (FIGURES 6–8). As in other species of Winteraceae, ray histology corresponds to Kribs's (1935) Heterogeneous Type I.

Growth rings are absent in *Belliolum* but present in *Pseudowintera* (Patel, 1974) and other species of Winteraceae from markedly temperate climates.

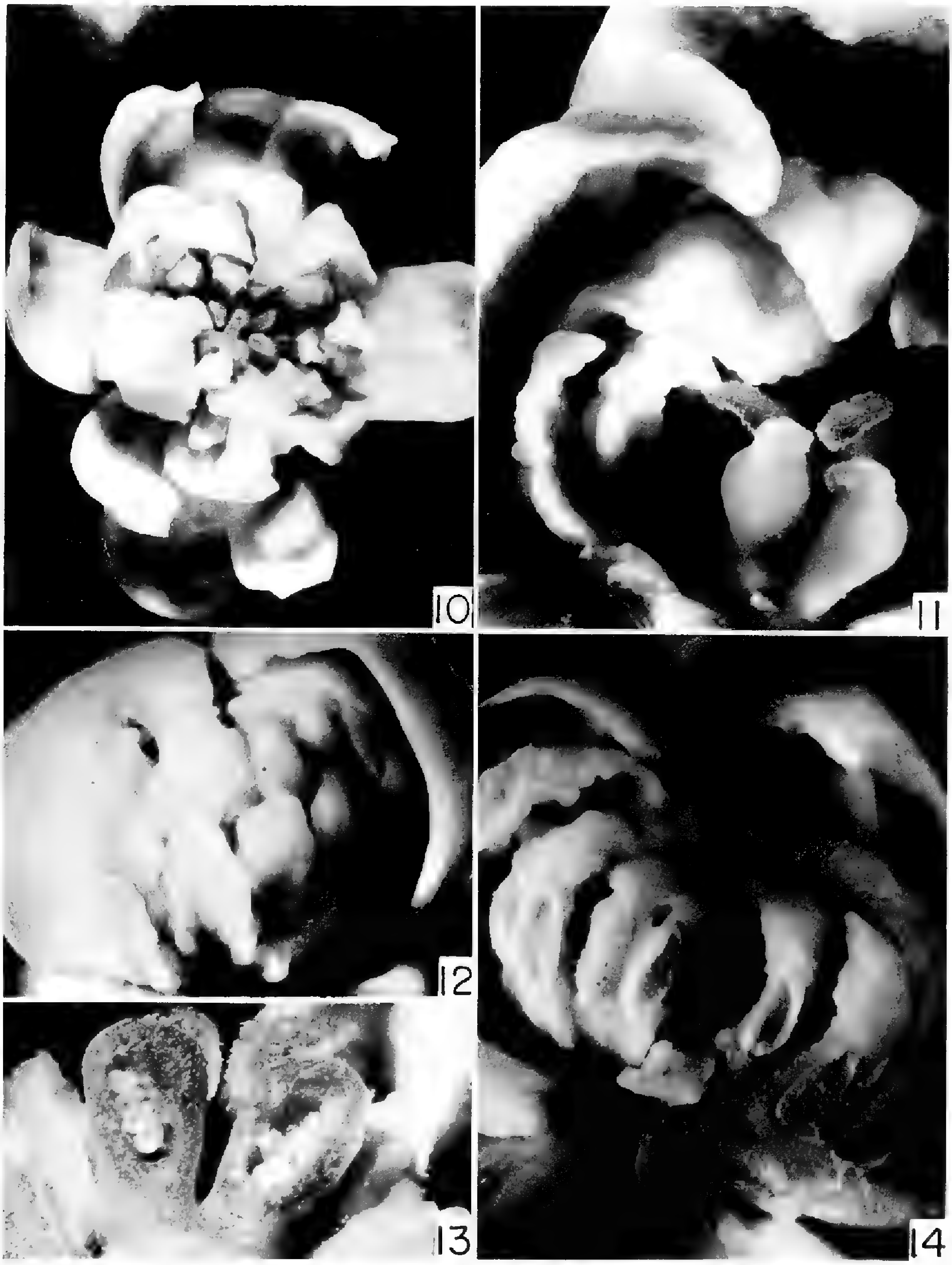
CONCLUSIONS

The species differ in tracheid length, probably in relation to size of plant. Bailey and Faull (1934) showed that tracheid length increases steadily with age in *Sequoia,* a pattern confirmed for other gymnosperms and for vesselless dicotyledons by Carlquist (1975). Tree (or shrub) size and trunk diameter appear to correlate with tracheid length. Tracheid diameter also appears to correlate with tracheid length in vesselless woods (Bannan, 1965). Compared to those of the other species studied here, the tracheids of *Belliolum gracile* are the longest (and widest); they were obtained from what is probably the largest tree (DBH = 20 cm) of the group. The longest tracheids (5580 μm) hitherto reported for vesselless angiosperms were from a sample of *Bubbia semecarpoides* that was 12 cm in diameter (Carlquist, 1975). Although trunk diameter and tracheid length are generally correlated (as they are in gymnosperms), the relation is not at all precise, as proved true in *Zygogynum* (Carlquist, 1981). Tracheids of *Agathis* are slightly longer than trunk diameter and plant height might suggest, but not greatly so (Carlquist, 1975). Süss (1980), who attempts to use tracheid length as a phylogenetic indicator in plants with vesselless wood, seems unaware of correlations between plant height and size and tracheid length (and diameter).

The differentiation of overlap areas in the tracheids of Winteraceae was noted by Bailey (1944) and has been illustrated for *Bubbia semecarpoides* and *Zygogynum bicolor* (as "*Z.* cf. *pomiferum*") (Carlquist, 1975), as well as for three other species of *Zygogynum* (Carlquist, 1981). As in *Belliolum,* scalariform end-wall pitting is clearly present in some collections of *Zygogynum* but absent in others. In *Pseudowintera* it is present only on enlarged traumatic tracheids (Patel, 1974). The presence of these scalariform pits on end walls in winteraceous tracheids has been claimed to be a kind of prevessel specialization of the tracheid for maximizing conductive ability (Carlquist, 1975, 1981). The presence on the end wall of scalariform pits rather than merely crowded circular pits may also be seen as a remnant of the capability—present in primitive vesselless woods—to produce scalariform pitting.

The range of axial parenchyma of *Belliolum* (diffuse and diffuse-in-aggregates, plus bands up to three cells wide in some collections) resembles that in *Zygogynum,* as does the typical ray width. The ray cells, however, do not show the division of labor (ethereal oil cells, sclereids) in *Belliolum* that they do in *Zygogynum.* The wood of *Belliolum* is less similar to that of *Pseudowintera,* as described by Patel, and most closely resembles those of *Bubbia* and *Zygogynum,* two genera phytogeographically closer to *Belliolum* than *Pseudowintera.* Some distinctive features of *Pseudowintera* (growth rings, helices in tracheids) are doubtless related to the strongly temperate climate of New Zealand, and thus the woods of *Bubbia, Belliolum,* and *Zygogynum* (which lack these features) reflect a mild and relatively seasonless climate.

On the basis of a limited number of samples, the Solomon Islands species of *Belliolum* differ from *B. pancheri* from New Caledonia. *Belliolum pancheri* has thicker-walled, narrower tracheids and narrower rays with thicker-walled cells than do the Solomon Islands species. Smith (1943) mentioned possible



FIGURES 10–14. **Belliolum pancheri:** 10, flower with stigmas receptive, × 2; 11, portion of flower at anthesis, × 6, dissected to show stamens (left) and carpels; 12, bud, dissected, × 4, showing stamens just prior to anthesis; 13, two carpels in longitudinal section, × 7.5, ovules in carpel at right displaced by sectioning; 14, dissection of flower at late anthesis, × 6, showing anthers open.

sectional differences between the Solomon Islands and New Caledonian groups of species on the basis of carpel morphology; xylarly characters might be taken into account in this connection. Bongers (1973) mentioned that stomata are much more deeply sunken in leaves of *B. crassifolium* (Baillon) Van Tieghem, a New Caledonian species, than they are in leaves of *B. haplopus,* from the Solomon Islands.

A NOTE ON FLOWERING

Thien (1980) has described the stages of anthesis in various Winteraceae, including *Belliolum.* FIGURES 10–14, photographs of *B. pancheri* taken in New Caledonia, illustrate additional aspects.

The opening mechanism of the flower of *Belliolum* is hygrochastic, or dependent upon swelling of the flower rather than drying for opening to occur. Dissection of a bud (FIGURE 12) reveals petals and stamens to be relatively thin and smooth before anthesis. By the time when anthesis occurs, however, the petals and stamens have enlarged appreciably and have developed ridges and warts (FIGURES 10, 11, 14). The deltoid stamen tips may thus play a role in the opening of the flower. During early anthesis the deltoid tips of the innermost stamens often appear to fit between the stigmas, so that the stigmas are exposed with certainty. The stamens soon reflex away from the carpels, however. The anther sacs are more nearly lateral than adaxial, but may be described as extrorse-latrorse (FIGURES 12, 14). Damage to anther tips by a chewing insect was noted (FIGURE 14). Sectioning the carpels (FIGURE 13) revealed that ovules are clearly positioned on the adaxial side of the locule, although the stigma extends down very little from the apex onto the adaxial face of the carpel. The stigmas would not be exposed at anthesis, because of carpel number and carpel crowding, if they were on adaxial faces; thus, one should expect the stigmas to be mostly apical in orientation in this genus. In the Solomon Islands species of *Belliolum* (Smith, 1942, 1943), the stigmas are even more clearly apical in nature than in *B. pancheri,* although the ovule position may be the same (Bailey & Nast, 1943).

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SYSTEMATICS OF THE ANDROPOGON VIRGINICUS COMPLEX (GRAMINEAE)

CHRISTOPHER S. CAMPBELL

THE ANDROPOGON VIRGINICUS COMPLEX is a closely interrelated group of nine species that range over much of the northern half of the New World (MAP 1). These grasses are weedy, diploid, sexual, cespitose perennials. The taxonomy of the broomsedges, as they are commonly called, has been confounded by the paucity and subtlety of taxonomically useful morphological characters and by the strong similarity of many of the taxa. Moreover, chromosome number and flavonoid chemistry have not provided additional usable variation. In this study, taxonomic rank is therefore based on morphological distance, supported by ecological and geographic differences. On the basis of extensive field observations and laboratory and herbarium study of the plants, twenty taxa are recognized. Four of the nine species include two or more varieties, and four of these varieties contain nine taxa, here called variants, that are not sufficiently distinct morphologically to warrant formal nomenclatural status. These variants have been given English names describing some aspect of their morphology, ecology, geography, or general nature. Six of the variants correspond to previously described taxa, and three are discussed here for the first time.

The center of diversity of the group, both for number of taxa and abundance of individual plants, is the Coastal Plain of the southeastern United States. The combination of effective wind dispersal of the fruit, frequent inbreeding, and relative competitive superiority makes the plants of the virginicus complex successful colonizers under conditions of density-independent mortality. Many of the taxa rapidly form large, dense populations wherever there is full sun and in all but the poorest and driest of soils. *Andropogon virginicus* L. var. *virginicus* dominates all other vegetation in the early stages of old-field succession in much of the eastern United States (Keever, 1950; Golley, 1965; Bazzaz, 1975). Like many other inbreeding, colonizing groups, the virginicus complex contains numerous taxa that are very similar morphologically (Stebbins, 1957; Lelong, 1965; Kannenberg & Allard, 1967).

These very similar taxa frequently grow together but rarely produce apparent

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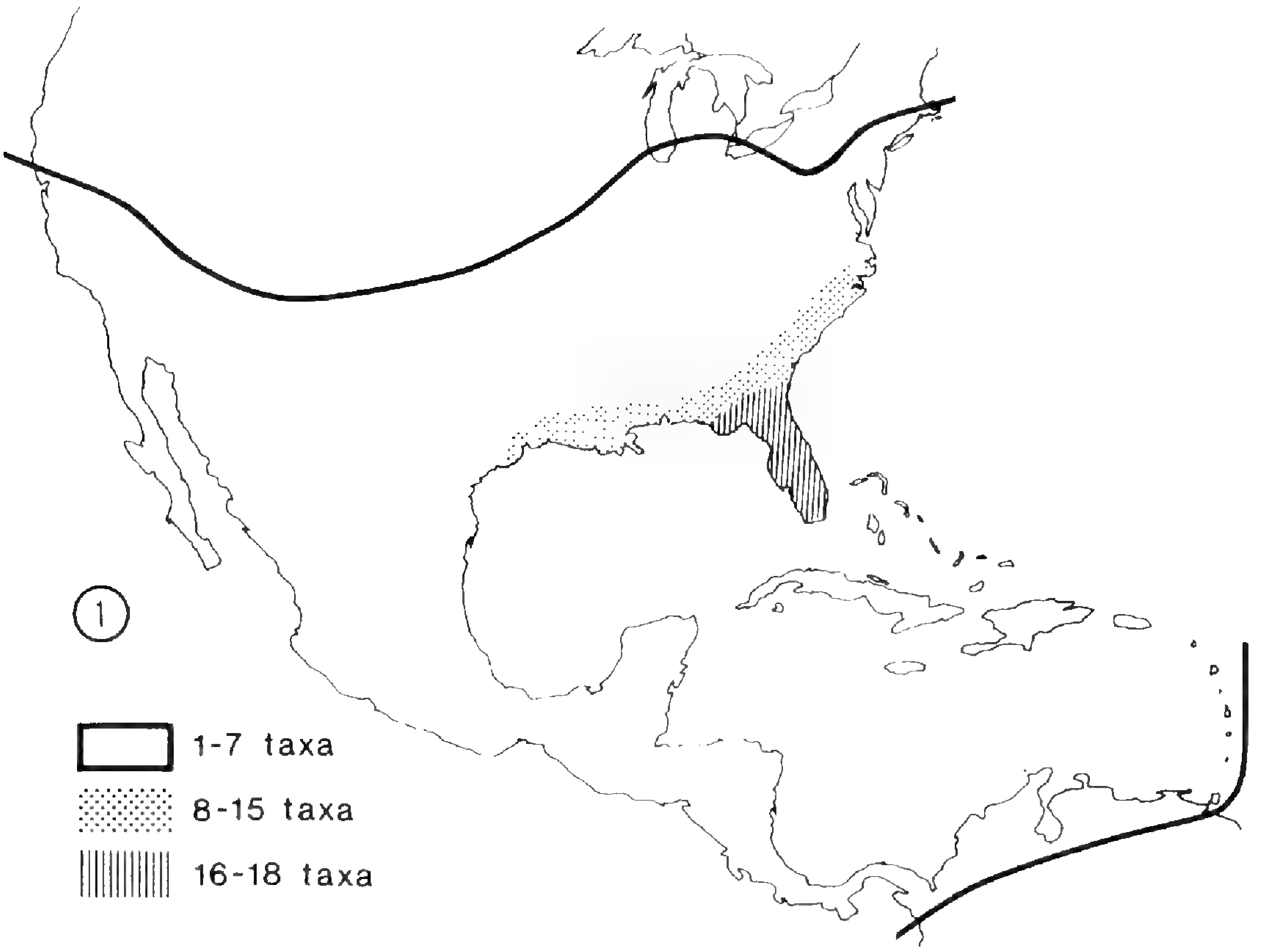


MAP 1. Distribution of the *Andropogon virginicus* complex.

hybrids (Campbell, 1980). They are effectively reproductively isolated from one another without being separated by large morphological gaps. These sibling species have been a taxonomic problem because, although they represent discrete variation, they are very difficult to distinguish. All of them belong to the three most widespread and weedy species, *Andropogon gyrans, A. virginicus,* and *A. glomeratus.* It is not surprising that authors of previous treatments of these species do not agree on the number of taxa that should be recognized (TABLE 1). Nash (1903) and Hitchcock (1951) overdescribed these species, and Roberty (1960), Radford *et al.* (1964), and Long and Lakela (1971) did not describe the variation sufficiently. Hackel (1889) and Fernald and Griscom (1935) misinterpreted some of the relationships within the virginicus complex, but the treatments by these authors provide the most insightful contributions to an understanding of the taxonomy of the group.

TAXONOMIC POSITION AND DEFINITION OF THE VIRGINICUS COMPLEX

The Linnaean concept of the genus *Andropogon* corresponds roughly to the current circumscription of the tribe Andropogoneae. The 12 species recognized by Linnaeus in the first edition of *Species Plantarum* are now distributed among nine genera.

The tribe is a natural assemblage, with a center of distribution in southeastern

TABLE 1. **Number of species (total taxa) recognized in previous taxonomic treatments of Andropogon gyrans, A. virginicus, and A. glomeratus, as delimited in this work.**

AUTHOR	SPECIES (total taxa) RECOGNIZED			
	gyrans	*virginicus*	*glomeratus*	Total
Hackel, 1889	1 (3)	1 (5)	1 (5)	3 (13)
Nash, 1903	3	4	3 (5)	10 (12)
Fernald & Griscom, 1935	1 (3)	1 (8)	0	2 (11)
Hitchcock, 1951	3	3 (4)	1	7 (8)
Roberty, 1960	0	1 (7)	0	1 (7)
Radford *et al.*, 1964	2	1	0	3
Long & Lakela, 1971	2	2 (3)	1	5 (6)
Campbell (present paper)	1 (3)	1 (5)	1 (5)	3 (13)

Asia (Hartley, 1950, 1958), and its cohesiveness rests on similarity in many aspects of morphology (Clayton, 1972), cytology (Celarier, 1956, 1957, 1958, 1959), anatomy (Metcalfe, 1960; Chaudra & Saxena, 1964; F. W. Gould, 1967), and biochemistry (Guttierrez *et al.*, 1974). It has been the focus of several major taxonomic studies (Hackel, 1889; Keng, 1939; Roberty, 1960) and has been considered the most advanced tribe of the Gramineae. If one agrees with Stebbins (1974), it is the most advanced taxon of all angiosperms.

Although the tribe is easily circumscribed, the delimitation of its genera has been problematic. Clayton (1972) used a numerical approach based on 41 morphological characters to cluster the genera. He admitted that his findings were tentative and that much remained to be done. For *Andropogon* he accepted Stapf's (1919) classification (1967, and pers. comm.). His concept of the genus is narrow and does not include *Bothriochloa* Kuntze, *Dichanthium* Willimet, or *Schizachyrium* Nees. However, the genus remains large and heterogeneous (F. W. Gould, 1967). The largest of Stapf's four sections, LEPTOPOGON Stapf, contains approximately 55 species (Clayton, pers. comm.), with about 20 in Africa and the balance in the New World. The complex of species centering around *A. virginicus* includes the majority of species of the section that occur in the northern areas of the New World.

Only three species of sect. LEPTOPOGON not included in the virginicus complex have been collected in the United States. *Andropogon ternarius* Michaux (including *A. ternarius* var. *cabanisii* (Hackel) Fernald & Griscom) is common in much of the eastern United States and rare in Mexico. *Andropogon bicornis* L., widespread in South and Central America and the West Indies, has been collected only once in the United States (Florida, Monroe County, *Craighead s.n.*, 1962 (FTG)). *Andropogon gracilis* Sprengel is rather frequent on the Miami oolite of Dade and Monroe counties, Florida. *Andropogon gerardii* Vitman and *A. hallii* Hackel of sect. ANDROPOGON are the only other species of the genus in the United States. South of the United States, 12 other species of sect. LEPTOPOGON occur within the range of the virginicus complex. *Andropogon virgatus* Desv. (probably better treated as *Hypogynium virgatum* (Desv.) Dandy) is morphologically the most distant of these species and will not be considered further. The nine other species outside the virginicus complex in the West Indies are *A. urbanianus* Hitchc., *A. gracilis, A. reedii* Hitchc. & Ekman, *A. reinoldii* León, *A. nashianus* Hitchc., *A. lateralis* Nees, *A. leucostachyus* HBK., *A. selloanus* (Hackel) Hackel, and *A. bicornis.* The last four also grow in Central America, and in Mexico along with three Mexican endemics, *A. bourgaei* Hackel, *A. pringlei* Scribner, and *A. spadiceus* Swallen. The four species that occur both east and west of the Gulf of Mexico also extend into South America. The section is well represented there, but only one species, *A. arenarius* Hackel, is very similar to species of the virginicus complex. Finally, *A. leucostachyus* is the only species found in both the New and Old Worlds (possibly introduced into Africa (Stapf, 1919)). Three African species of sect. LEPTOPOGON, *A. eucomus* Nees, *A. huillensis* Rendle, and *A. laxatus* Stapf, resemble the species of the virginicus complex in general aspect but are excluded from the complex on morphological grounds (see below).

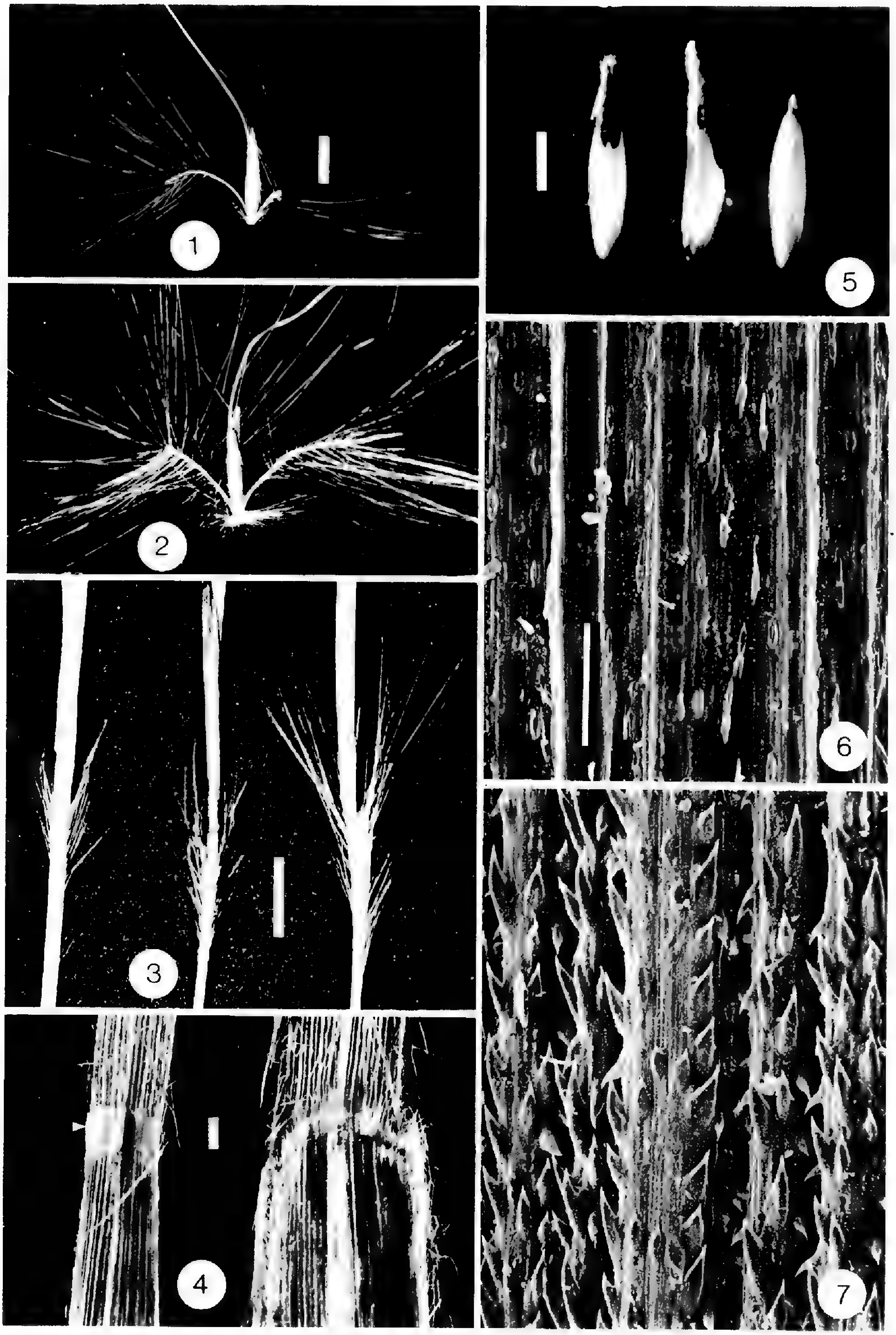
The essential features characterizing all the taxa of the virginicus complex and combining to distinguish them from the other species of sect. LEPTOPOGON are presented in TABLE 2. The reduction in stamen number from three to one, the single most distinctive feature of members of the virginicus complex, is found in many other genera of grasses: *Cinna* L., *Uniola* L. (Booth, 1964), *Stipa* L. (Brown, 1949), *Bothriochloa* (Heslop-Harrison, 1961), *Briza* L. (Murray, 1974), *Imperata* Cyr. (Clifford, 1961), *Deschampsia* Beauv. (Parodi, 1949), *Chikusichloa* Koidz. (Connor, 1979), *Poa* L. (Weatherwax, 1929), and *Vulpia* K. C. Gmelin (Cotton & Stace, 1977). In these genera, as in the virginicus complex, the reduction in stamen number is associated with the capacity for cleistogamy (Campbell, 1982b). The only other species with one stamen in sect. LEPTOPOGON are *Andropogon gracilis* and the two closely related Mexican endemics, *A. pringlei* and *A. spadiceus.* Significantly, all three produce cleistogamous flowers, although cleistogamy in these taxa differs from that in the virginicus complex (Campbell, 1982b). Because *A. gracilis* has one raceme per inflorescence unit, several authors have placed it in *Schizachyrium* (*S. gracile* (Sprengel) Nash). However, it does not have the cupuliform rachis internodes and rounded glumes of the sessile spikelets that Clayton (1964) considered to be important features of *Schizachyrium.* In addition to having solitary racemes, *A. gracilis* differs from the virginicus complex in being tetraploid ($n = 20$; Davidse & Pohl, 1972). *Andropogon pringlei* and *A. spadiceus* differ from the virginicus complex in three morphological characters (TABLE 2).

Of the 16 species listed in TABLE 2, only *Andropogon huillensis* is separated from the virginicus complex in less than two ways. There may be a second difference for this species, depending upon what its chromosome number really is (two different ploidy levels have been reported—see TABLE 2). Six species differ in only two ways. The wide-ranging *A. lateralis* (and the numerous species closely related to it) is quite different from the virginicus complex in having large, functional, pediceled spikelets. For some of the other five species listed in TABLE 2, there are additional differences that are not given in the table. The racemes of *A. selloanus* and *A. eucomus* are more densely pubescent. The lower glumes of *A. nashianus* are ovate in shape and distinctly different from the lanceolate to oblong lower glumes of plants of the virginicus complex. Mor-

TABLE 2. **Comparison of the Andropogon virginicus complex with its closest relatives.**

SPECIES	STAMEN NUMBER	SPIKELET LENGTH (mm)	AWN	AWN BASE TWISTING	PEDICELED SPIKELET	RACHIS INTERNODE	CHROMOSOME NUMBER
A. virginicus complex	1	3–5	Present	Moderate	0 to vestigial	Thin	$n = 10$*
A. arenarius	3	4–6	Usually absent	—	0 to functional	Thin	Unknown
A. bicornis	3	3–4	Absent	—	0 to functional	Thin	$n = 30$ (Pohl & Davidse, 1971)
A. bourgaei	3	ca. 4	Absent	—	0 to functional	Thin	Unknown
A. eucomus	3	2.5–3	Present	Moderate	0 to vestigial	Thin	$n = 10$ (de Wet, 1954)
A. huillensis	3	ca. 4	Present	Moderate	0 to vestigial	Thin	$n = 30$ (de Wet, 1960) $n = 10$ (Dujardin, 1978)
A. lateralis	3	3.5–5	Present	Moderate	0 to functional	Thin	Unknown
A. laxatus	3	4–5	Present	Strong	0 to vestigial	Thin	Unknown
A. leucostachyus	3	2.5–3.5	Absent	—	0 to vestigial	Thin	$n = 10$ (F. W. Gould, 1956)
A. nashianus	3	2.5–3.5	Present	Moderate	0 to vestigial	Thin	Unknown
A. pringlei/spadiceus	1	6–7	Present	Strong	0 to vestigial	Thick	Unknown
A. reedii	3	4–6	Present	Strong	0 to functional	Thin	Unknown
A. reinoldii	3	2.5–3	Present	Moderate	0 to vestigial	Thin	Unknown
A. selloanus	3	ca. 4	Absent	—	0 to vestigial	Thin	$n = 10$ (F. W. Gould, 1956)
A. ternarius	3	5–6.5	Present	Moderate	0 to vestigial	Thick	$n = 20$ (F. W. Gould, 1956)
A. urbanianus	3	4–6	Present	Strong	0 to functional	Thin	$n = 40$ (Davidse & Pohl, 1972)

*See Table 3.



FIGURES 1–7. 1, 2, dispersal units, scale bar = 2 mm: 1, old-field variant of *Andropogon virginicus* var. *virginicus* (*Campbell 3770*); 2, common variant of *A. gyrans* var. *gyrans* (*Campbell 3782*). 3, bases of raceme sheaths showing sparse, moderate, and dense pubescence, bar = 2 mm. 4, ligules (arrow) of *A. glomeratus* var. *glomeratus* (left, *Camp-*

phologically, *A. huillensis, A. reinoldii,* and *A. laxatus* remain as the species closest to the virginicus complex.

The uniformity of the virginicus complex in the features shown in TABLE 2 argues for its naturalness. Other evidence for this supposition comes from the chemical similarity of the taxa. Eighteen of the taxa were surveyed with standard methods of paper chromatography (Mabry *et al.*, 1970): sixteen had nearly identical spot patterns. The two that vary somewhat, *Andropogon arctatus* and the robust variant of *A. glomeratus* var. *pumilus,* differ from the remainder of the virginicus complex in other ways as well. *Andropogon arctatus* has rhizomes, the most primitive flowering mode of the virginicus complex, and a different sort of life history. The robust variant has the widest tolerance for soil salinity and pH of all taxa of the virginicus complex.

GENERAL DESCRIPTION OF THE VIRGINICUS COMPLEX

The yearly growth of plants of the virginicus complex is divided into two phases. In the first part of the season, growth is vegetative in the form of a proaxis of basal leaves with very shortened internodes. In July, August, or September (presumably in response to short day-length, as in other species of the Andropogoneae (Tompsett, 1976)), the proaxis extends rapidly to produce a flowering stem. The stems are terete and 0.2–3.1 m in height.

The leaves may be glabrous or pubescent with unicellular macrohairs; scabrous on the adaxial blade surface and, in some taxa, on the abaxial sheath surface; and glaucous or green. The leaf blades are flattened to occasionally folded, and laxly recurving to infrequently erect. The ligules[1] are membranaceous and 0.2–2.2 mm long, with margins glabrous to long-ciliate.

The inflorescence is a complex branch system. Stapf (1919) described the branching of *Andropogon* as cymose. At each node of plants of the virginicus complex, one to eleven branches may develop on a very short common axis. The largest branch is next to the parent axis, and successively smaller ones arise distally on the common axis. The branches alternate in two ranks that are close to one another on the adaxial side of the common axis. The first structure on the common axis is a two-nerved, hyaline prophyll separating the first branch from the parent axis. Between each of the distal branches there is also a prophyll (FIGURE 10).

The tips of the ultimate branches of the inflorescence bear structures here called inflorescence units (see APPENDIX A and FIGURE 11). The raceme sheath

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[1] Certain terms, of a technical nature or specialized in their meaning, are frequently used in this paper. They are defined in APPENDIX A, and some are illustrated in FIGURES 1–11.

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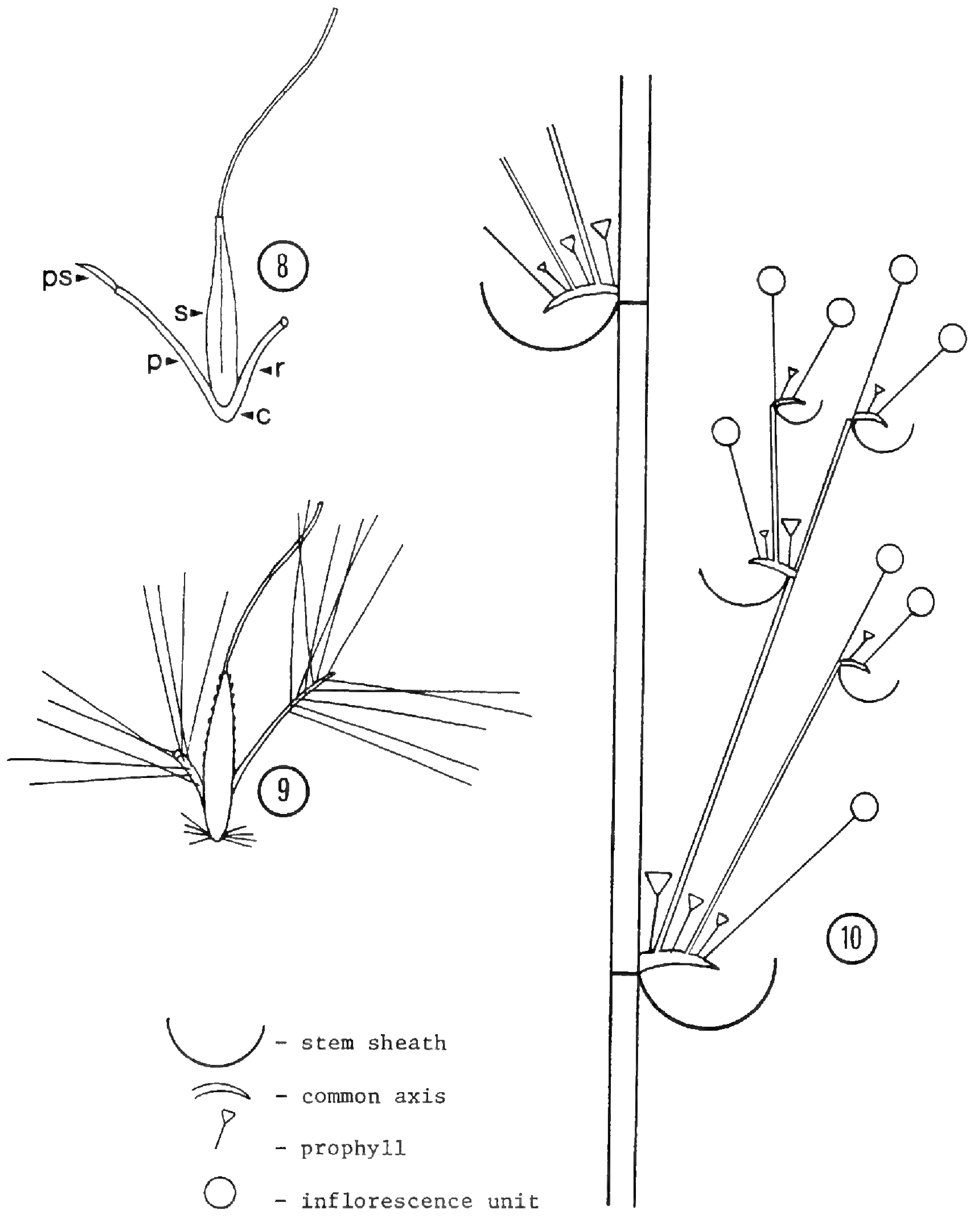
bell 3805) and deceptive variant of *A. virginicus* var. *virginicus* (right, *Campbell 3747*), bar = 1 mm. 5, fruits of common variant of *A. gyrans* var. *gyrans* (*Campbell 3872*) (note marcescent anther at apex of left and center fruits), bar = 1 mm. 6, 7, scanning electron micrographs of stem sheaths, scale bar = 1 μm: 6, deceptive variant of *A. virginicus* var. *virginicus* (*Campbell 3870*) (note bicellular microhairs); 7, *A. glomeratus* var. *glomeratus* (*Campbell 3973*) (note apically directed prickle hairs).



FIGURES 8–10. 8, 9, dispersal units: 8, old-field variant of *Andropogon virginicus* var. *virginicus* (pubescence not included), showing one-keeled upper glume and base of awn; 9, robust variant of *A. glomeratus* var. *pumilus* (many hairs of callus, rachis internode, and pedicel omitted), showing two-keeled lower glume (note prickle hairs extending to below middle of keels of lower glume). 10, diagram of inflorescence node of plant of virginicus complex. c = callus, p = pedicel, ps = pediceled spikelet, r = rachis internode, s = spikelet.

subtends the peduncle, which bears at its apex two or more racemes. The raceme is made up of a straight axis, the rachis, which has four to fourteen nodes. At each node there is a pair of spikelets (a major character for the tribe Andropogoneae). In the virginicus complex, one of the spikelets is sessile and the other is vestigial or entirely absent and represented only by its pedicel. The sessile spikelet has two subcoriaceous glumes. The lower glume has two keels, and the upper glume has one. The glumes enclose two florets, the lower of which is sterile (as in most members of subfam. Panicoideae) and is represented only by a hyaline lemma. The upper floret consists of a long-awned, hyaline lemma, a vestigial (0.4–1.5 mm long) palea, and a flower with two lodicules, one stamen, and a two-styled ovary. The ovary matures into a brownish or purplish caryopsis.

FLOWERING

The 15 taxa observed flower consistently around dawn in the late summer and early fall. Populations in the northeastern United States tend to flower in August and September, and those in the south from September to November. In any region there is great overlap in flowering time between most of the taxa. Exceptions are noted under individual taxa. Vernal flowering occurs in some taxa (e.g., *Andropogon brachystachyus* and especially *A. longiberbis*), apparently in response to burning. In Mexico, Central America, and the West Indies late summer to fall flowering predominates.

Variation in flowering in the virginicus complex is considerable (Campbell, 1982b). *Andropogon arctatus, A. tracyi, A. floridanus, A. brachystachyus,* and some taxa of *A. virginicus* and *A. glomeratus* produce mostly chasmogamous flowers (see character 33 of TABLE 4). The synchrony of peduncle elongation and floral maturation exposes the spikelets above the raceme sheath at anthesis. The lodicules can then open the spikelet. The filament elongates in about an hour, and the anther and styles protrude for potential cross-pollination. If the peduncle does not elongate sufficiently to free the spikelet above the raceme sheath, the lodicules cannot open the spikelet, and cleistogamy results.

When the peduncle does not elongate appreciably, the combined action of many lodicules forces the racemes out between the margins of the raceme sheath. The lodicules then open the spikelets. If, however, the flowers mature before the inflorescence unit emerges from the stem sheath in which it developed, the lodicules cannot open the spikelets. Cleistogamy is far more common in short-peduncled than in long-peduncled racemes (see character 33 of TABLE 4).

CHROMOSOME NUMBERS

Counts of a haploid chromosome number of 10 have been made for all species and for 16 of the 21 taxa (TABLE 3). Because of the possibility of misidentification of these morphologically close grasses, published reports are less reliable than those for which a voucher has been examined. The two polyploid counts reported for *Andropogon virginicus* are strongly questioned because of the uniform diploidy of the complex. The count of $2n = 40$ may have been based on a mitotic division in the anther similar to the one shown in FIGURE 16. The chromosomes appear to be meiotic, and the nucleolus marks

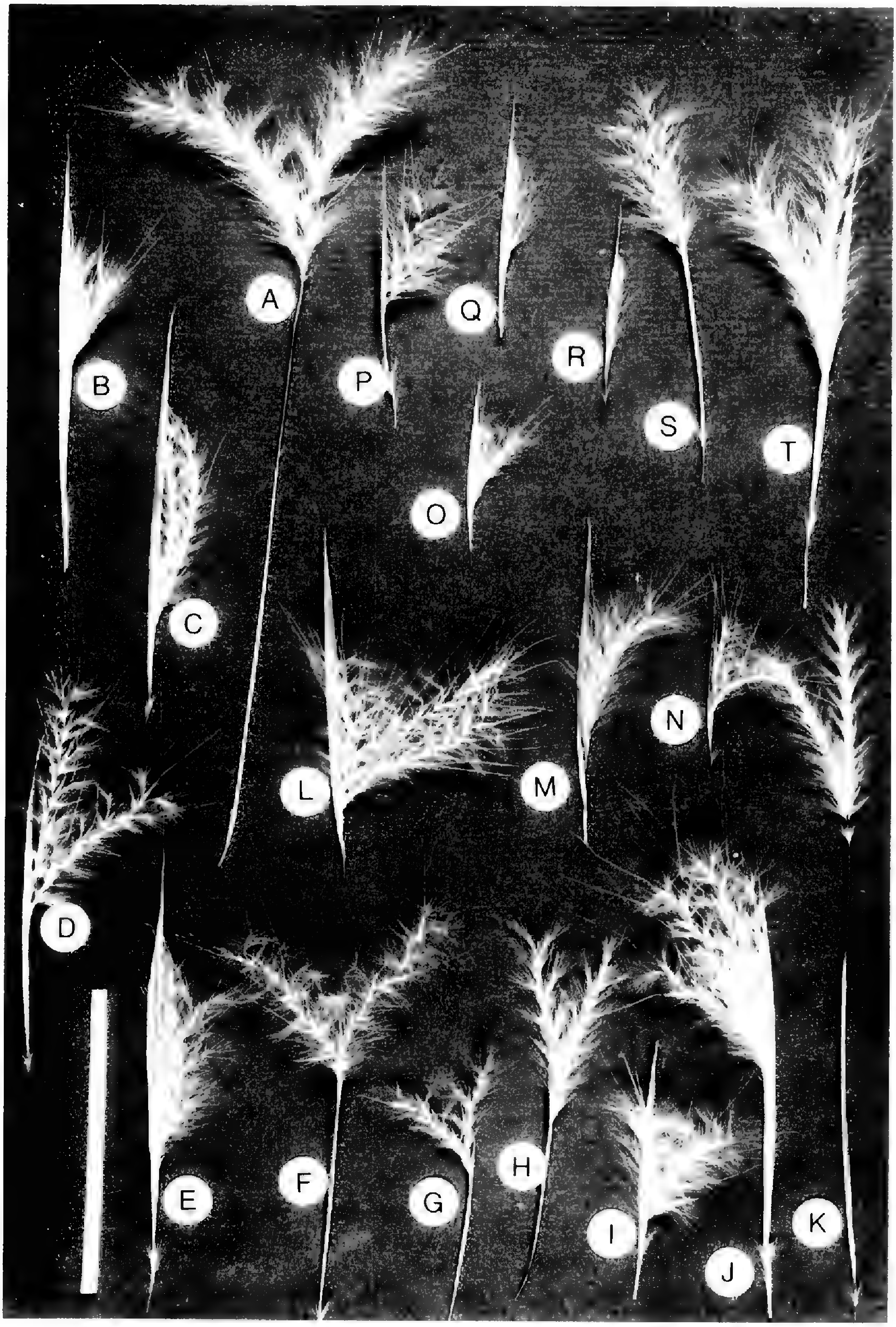


FIGURE 11. Inflorescence units: A, B, common variant of *Andropogon gyrans* var. *gyrans* (*Campbell 3872*); C, D, *Andropogon gyrans* var. *stenophyllus* (*Campbell 3822*); E, F, tenuous variant of *A. gyrans* var. *gyrans* (*Campbell 3873*); G, *A. brachystachyus* (*Campbell 3884*); H, *A. floridanus* (*Campbell 3754*); I, *A. longiberbis* (*Campbell 3729*); J, *A. liebmannii* var. *pungensis* (*Campbell 3948*); K, *A. arctatus* (*Campbell 3944*); L, M,

the stage as prophase, but another cell from the same anther, a pollen mother cell in prophase I, showed ten bivalents.

For the 16 counts reported in this work, young spikelets were fixed in Farmer's solution (3 parts 100% ethyl alcohol, 1 part glacial acetic acid), transferred to 70% ethyl alcohol after 24 hours, and stored at about 4°C. Fixation early in the morning yielded far more meiotic figures than that done later in the day. The ten new counts reported here are shown in FIGURES 12–21. In all taxa studied the basipetal sequence of floral maturation facilitated finding prophase I to anaphase I. In racemes of wholly chasmogamous flowers, the developmental gradient is steeper than in those with cleistogamous flowers. In the former group, one raceme may contain nearly mature pollen in the apical spikelets and pollen mother cells in the basal spikelets. In contrast, meiosis may occur concurrently in all flowers of a raceme in the frequently or predominantly cleistogamous taxa.

GEOGRAPHIC DISTRIBUTION

Eighteen of the taxa grow on the Coastal Plain of the southeastern United States (see MAP 1). The distribution of 12 is entirely limited to the region extending from southernmost New Jersey to eastern Texas. *Andropogon arctatus, A. floridanus, A. longiberbis,* and *A. brachystachyus* grow principally in Florida and infrequently in nearby states or the Bahamas. Only one taxon of eastern United States broomsedges, *A. liebmannii* var. *pungensis,* does not occur extensively in Florida.

The common variant of *Andropogon gyrans* var. *gyrans,* the old-field variant of *A. virginicus* var. *virginicus,* the robust variant of *A. glomeratus* var. *pumilus,* and the two varieties of *A. liebmannii* show a pattern of eastern United States–Mexican distributions common to many other vascular plants (Graham, 1973). Because of the uncertainties about the phytogeographic relationships of these two regions and the paucity of andropogonoid fossils, assertions concerning the direction of migration are conjectural. However, one line of reasoning suggests migration from the center of distribution to Mexico. This rests on the hypothesis (developed more fully in the discussion under *A. brachystachyus*) that *A. virginicus* is derived from *A. brachystachyus* ancestry. The range of the latter taxon and most of the variants of *A. virginicus* is restricted to the southeastern United States. Only the old-field variant of var. *virginicus* grows in Mexico, possibly after migration there.

Closely related taxa in *Andropogon virginicus* and *A. glomeratus* have the

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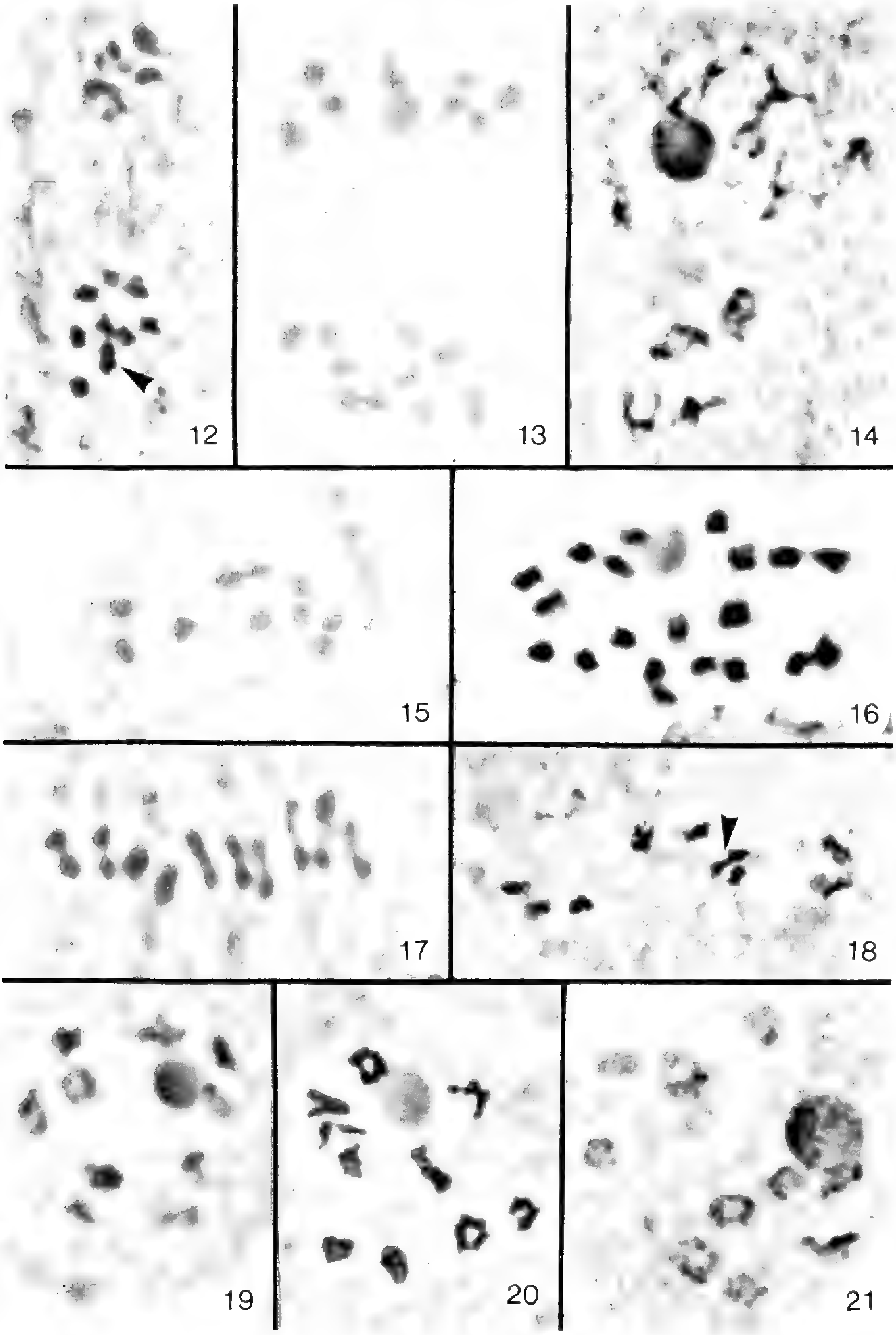
old-field variant of *A. virginicus* var. *virginicus* (*Campbell 3849*); N, deceptive variant of *A. virginicus* var. *virginicus* (*Campbell 4081*); O, drylands variant of *A. virginicus* var. *glaucus* (*Campbell 3898*); P, robust variant of *A. glomeratus* var. *pumilus* (*Campbell 3850*); Q, *A. glomeratus* var. *hirsutior* (*Campbell 3804*); R, *A. glomeratus* var. *glaucopsis* (*Campbell 3806*); S, *A. glomeratus* var. *glomeratus* (*Campbell 3915*); T, *A. tracyi* (*Campbell 4100*). Bar = 5 cm.

TABLE 3. **Chromosome numbers in the Andropogon virginicus complex.**

TAXON	COUNT	LOCALITY	VOUCHER SPECIMEN OR REFERENCE
A. **arctatus**	$n = 10$	Florida, Liberty Co.	*Campbell 4060* (GH)
A. **brachystachyus**	$n = 10$	Florida, Putnam Co.	*Campbell 4264* (GH)
A. **floridanus**	$2n = 20$	No locality given	Carnahan & Hill, 1961
	$n = 10$	Florida, Marion Co.	*Campbell 4194* (GH)
A. **glomeratus**	$n = 10$	No locality given	Church, 1936
var. **glaucopsis**	$2n = 20$	Florida, Duval and St. Johns cos.	Church, 1940
var. **glomeratus**	$n = 10$	Massachusetts, Plymouth Co.	*Campbell 3973* (GH)
	$2n = 20$	Rhode Island, Washington Co.	Church, 1940
var. **hirsutior**	$n = 10$	Georgia, Berrien Co.	*Celarier* (MO)
		Alabama, Baldwin Co.	*Campbell 3804* (GH)
var. **pumilus**			
robust variant	$n = 10$	Texas, Fort Bend Co.	F. W. Gould, 1956
		Georgia, Berrien Co.	*Celarier A-2600-1* (MO)
		Alabama, Montgomery Co.	*Campbell 3958* (GH)
		No locality given	*Gage s.n.* (MO)
		Mexico, Veracruz	*Campbell 3648* (GH)
		Dominican Republic, Espaillat	Davidse & Pohl, 1972
	$2n = 20$	Texas, Robertson Co.	Church, 1940
		Texas, no county given	Brown, 1950
		Mexico, Chiapas	F. W. Gould & Soderstrom, 1970
A. **gyrans**			
var. **gyrans**			
common variant	$n = 10$	Louisiana, Rapides Parish	*Gould RF 506* (TAES)
		Georgia, Tift Co.	*Celarier A-2608-1* (MO)
		Florida, Jackson Co.	*Campbell 3815* (GH)

	$2n = 20$	Georgia, McIntosh Co. Mexico, Chiapas	Church, 1940 Tateoka, 1962
tenuous variant	$n = 10$	Florida, Highlands Co.	*Campbell 3746* (GH)
var. **stenophyllus**	$n = 10$	Florida, Liberty Co.	*Campbell 4259* (GH)
A. longiberbis	$n = 10$	Florida, Dade Co.	*Campbell 3734* (GH)
A. liebmannii			
var. **pungensis**	$n = 10$	Alabama, Washington Co.	*Campbell 3695* (GH)
A. tracyi	$n = 10$	Florida, Putnam Co.	*Campbell 4100* (GH)
A. virginicus			
var. **glaucus**			
wetlands variant	$n = 10$	Florida, Jackson Co.	*Campbell 3818* (GH)
var. **virginicus**	$n = 10$	Massachusetts, Barnstable Co. Texas, Robertson and San Augustine cos.	Church, 1936 F. W. Gould, 1956
	$2n = 20$	Virginia, Princess Anne Co.	Church, 1940
	$2n = 40$*	Tennessee, no county given	*Alava 3246, 3252* (MO)
	$n = 40$*	No locality given	Mohlenbrock, 1973
deceptive variant	$n = 10$	Florida, Jackson Co.	*Campbell 3778* (GH)
old-field variant	$n = 10$	Rhode Island, Washington Co. Georgia, Berrien Co. Florida, Jackson Co. Florida, Putnam Co.	*Celarier A-2620-1* (MO) *Celarier A-2607-1* (MO) *Campbell 3782* (GH) *Campbell 4265* (GH)

*Probably misinterpretations.



FIGURES 12–21. Chromosomes (see TABLE 3 for voucher data; unless otherwise noted, all meiotic figures): 12, *Andropogon floridanus,* anaphase, × 720; 13, deceptive variant of *A. virginicus* var. *virginicus,* anaphase, × 720; 14, *A. tracyi,* diakinesis, × 720; 15, *A. liebmannii* var. *pungensis,* diakinesis, × 865; 16, *A. gyrans* var. *stenophyllus,* mitotic prophase in an anther, × 965; 17, *A. brachystachyus,* metaphase, × 825; 18, *A. longi-*

most similar ranges. The wetlands, drylands, deceptive, and smooth variants of the former and *Andropogon glomeratus* vars. *glaucopsis* and *hirsutior* are found on the Coastal Plain of the southeastern United States, especially from southern Virginia and Mississippi (MAPS 13–16, 18, 19).

ECOLOGY

The requirements of high levels of sunlight and little competition usually confine populations of the virginicus complex to areas undergoing early succession or to persistently disturbed sites; they characteristically grow along roadsides or under powerlines, or they invade abandoned agricultural land or clear-cut timberlands (FIGURES 22–27). The old-field variant of *Andropogon virginicus* var. *virginicus* is so successful as a colonizer (Keever, 1950; Golley, 1956; Bazzaz, 1975) that the three- to five-year period after an environmental opening has occurred is called the broomsedge stage.

The success of members of the virginicus complex as weeds is certainly due in part to their dispersibility, both locally and to newly available sites. The long, spreading hairs of the dispersal unit provide aerodynamic drag for wind dispersal; the terminal velocity of the dispersal units is roughly equivalent to that of the common dandelion (Campbell, 1983). Because they are considerably taller than dandelions, the individual broomsedge plants have a greater potential dispersal range. The probability of their long-distance dispersal increases through their capacity for autogamy. The increase in homozygosity that accompanies inbreeding apparently promotes close adaptation to a particular environment (Allard, 1975). The most successful colonizers of the virginicus complex—the common variant of *Andropogon gyrans* var. *gyrans,* the old-field and deceptive variants of *A. virginicus* var. *virginicus,* and *A. glomeratus* vars. *hirsutior* and *glaucopsis*—bear mostly cleistogamous flowers. The one notable exception to this generality is the robust variant of *A. glomeratus* var. *pumilus.*

These andropogons will flourish in partial shade if competition is suppressed through fire. In two pine plantations in the southeastern United States, there are extensive populations of the virginicus complex where annual burns prevent hardwood growth. Over large areas in both localities, the fall reproductive growth of the broomsedges dominates the undergrowth (FIGURE 26). At the plantation in Thomas County, Georgia, there are large populations of eight taxa of the complex, and at the Bladen County, North Carolina, site six taxa grow together. Clayton (1969) pointed to a possible adaptation for fire ecology of *Hyparrhenia* Andersson of the Andropogoneae in the demonstrated ability of their dispersal units to bury themselves. The hygroscopic awn and the callus

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berbis, diakinesis, × 715; 19, wetlands variant of *A. virginicus* var. *glaucus,* diakinesis, × 790; 20, tenuous variant of *A. gyrans* var. *gyrans,* diakinesis, × 940; 21, *A. arctatus,* diakinesis, × 715. (Arrows in 12 and 18 indicate two bivalents not resolvable in this focal plane.)

FIGURES 22–27. 22, 23, old-field variant of *Andropogon virginicus* var. *virginicus*: 22, under powerline, Kent Co., Maryland; 23, in four-year-old *Pinus elliottii* timberland, Decatur Co., Georgia. 24, *A. brachystachyus*, in clearing in flatwoods, Highlands Co., Florida. 25, clear-cut *P. clausa* timberlands colonized by *A. floridanus*. 26, several taxa

hairs work the spikelet into the soil, where it is more protected from fire. The broomsedge dispersal unit may function in the same way, although the awn is often barely twisted (and therefore weakly hygroscopic).

Most of the taxa of the virginicus complex have rather narrow tolerance for soil moisture. For example, in the panhandle of Florida, one characteristically finds the wetlands variant of *Andropogon virginicus* var. *glaucus* at the bottom of roadside ditches. *Andropogon gyrans* var. *stenophyllus* often borders the same ditches, and above the ditches one is likely to see the deceptive variant of *A. virginicus* var. *virginicus,* the common variant of *A. gyrans* var. *gyrans,* and the drylands variant of *A. virginicus* var. *glaucus.* The old-field variant of var. *virginicus,* tolerant of a wide variety of soil moisture conditions, may occur anywhere on the slope.

While human activity has been decidedly beneficial to these broomsedges, the plants are commercially undesirable since they supplant other vegetation of greater economic value as fodder. Cattle generally eschew most of these andropogons. The only direct economic value of the plants is in their leaves and stems, which have long been used for dyeing fabric and for brooms.

EVOLUTION AND SPECIATION

A dominant trend in the evolution of the virginicus complex has been the shift from chasmogamy to cleistogamy. Stebbins (1957) presented convincing evidence for the primitive nature of outcrossing and the derived condition of inbreeding. The derivation of cleistogamy in the virginicus complex involved shortening the peduncle and developmental shifts in the maturation of the flowers (Campbell, 1982b). Smaller spikelets and anthers and increased weediness are often associated with a shift toward cleistogamy. The reduction in anther length and pollen-producing capacity may result from relaxed selection for the copious pollen needed for wind pollination.

Evidence suggests that the change from chasmogamy to cleistogamy has repeatedly occurred in the virginicus complex (Campbell, 1982b). Both the tenuous variant of *Andropogon gyrans* var. *gyrans* and var. *stenophyllus* of the same species consist of two kinds of plants, one with some long peduncles and chasmogamous flowers and one with all short peduncles and mostly cleistogamous flowers. The plants are otherwise similar, but the cleistogamous form of both taxa is more widespread and common.

Another derivation of cleistogamy involves the precocious sexual maturation of ancestors of *Andropogon brachystachyus* to produce the deceptive variant of *A. virginicus* var. *virginicus* and, by other character changes, the rest of *A. virginicus.* Finally, *A. glomeratus* var. *glomeratus* appears to be the ancestral stock for both vars. *hirsutior* and *glaucopsis.*

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of *A. gyrans, A. virginicus,* and *A. glomeratus* in annually burned *P. palustris* plantation, Thomas Co., Georgia. 27, robust variant of *A. glomeratus* var. *pumilus* in roadside ditch, Putnam Co., Florida.

Cleistogamy presumably brings to the virginicus complex both greater colonizing ability (see ecology section) and a barrier to gene flow between the taxa (Campbell, 1982b). This barrier contributes to the reproductive isolation of the taxa that grow together. Mixed populations of broomsedges are so common now that one might assume that they have always grown together and that speciation was sympatric. Cleistogamy might have provided the interruption in gene flow essential to divergence. However, the phenomenon of mixed populations may have developed largely in the presence of man's tremendous disturbance of the habitat. The taxa that are so common today may once have been restricted to infrequent openings caused by fire and other natural disturbance. Their divergence from one another may have taken place in isolation in pre-Columbian times.

Many of the taxa that frequently grow near one another in mixed populations are very closely related. For example, two varieties of *Andropogon glomeratus,* vars. *hirsutior* and *glaucopsis,* form mixed populations in 67 percent of the 28 populations I have studied (Campbell, 1980). I have not detected plants of intermediate morphology that would suggest gene flow between these or most of the other closely related taxa.

HYBRIDIZATION

Hybridization between taxa of the virginicus complex is rare. There are ample opportunities for gene flow between taxa because they frequently grow together and flower at the same time of day and (mostly) at the same time of year. I have observed two taxa growing within one to three meters of one another over four hundred times. In only five of these opportunities for hybridization were there plants whose intermediate morphology suggested that they were hybrids. In the rare instances when hybridization does take place, there are few mature hybrid individuals. I have found only twelve putative hybrid individuals in the five localities where hybridization is suspected. The parents outnumber these hybrids by between five and one hundred or more to one.

Four of the suspected hybridizations involve the old-field variant of *Andropogon virginicus* var. *virginicus. Andropogon longiberbis* and the robust variant of *A. glomeratus* var. *pumilus* are the other parents in two cases each. In the fifth instance the robust variant and *A. longiberbis* produced six putative F_1 plants.

In all these instances the putative hybrids are morphologically intermediate between the parents. The three putative F_1 hybrids of the old-field variant and *Andropogon longiberbis* fall between the parents in the orientation of sheath pubescence, the number of racemes per inflorescence unit, and the lengths of the racemes, spikelets, and callus hairs. The three putative hybrids of the old-field and robust variants are intermediate in leaf-blade and raceme-sheath width and in maximum number of inflorescence branches. In leaf-blade length and number of inflorescence units per stem, however, the hybrids from both populations exceed the mean of these characters for both parents. For the robust variant and *A. longiberbis* there are ten characters distinguishing the parents for which the putative hybrids are more or less intermediate: stem height, leaf-

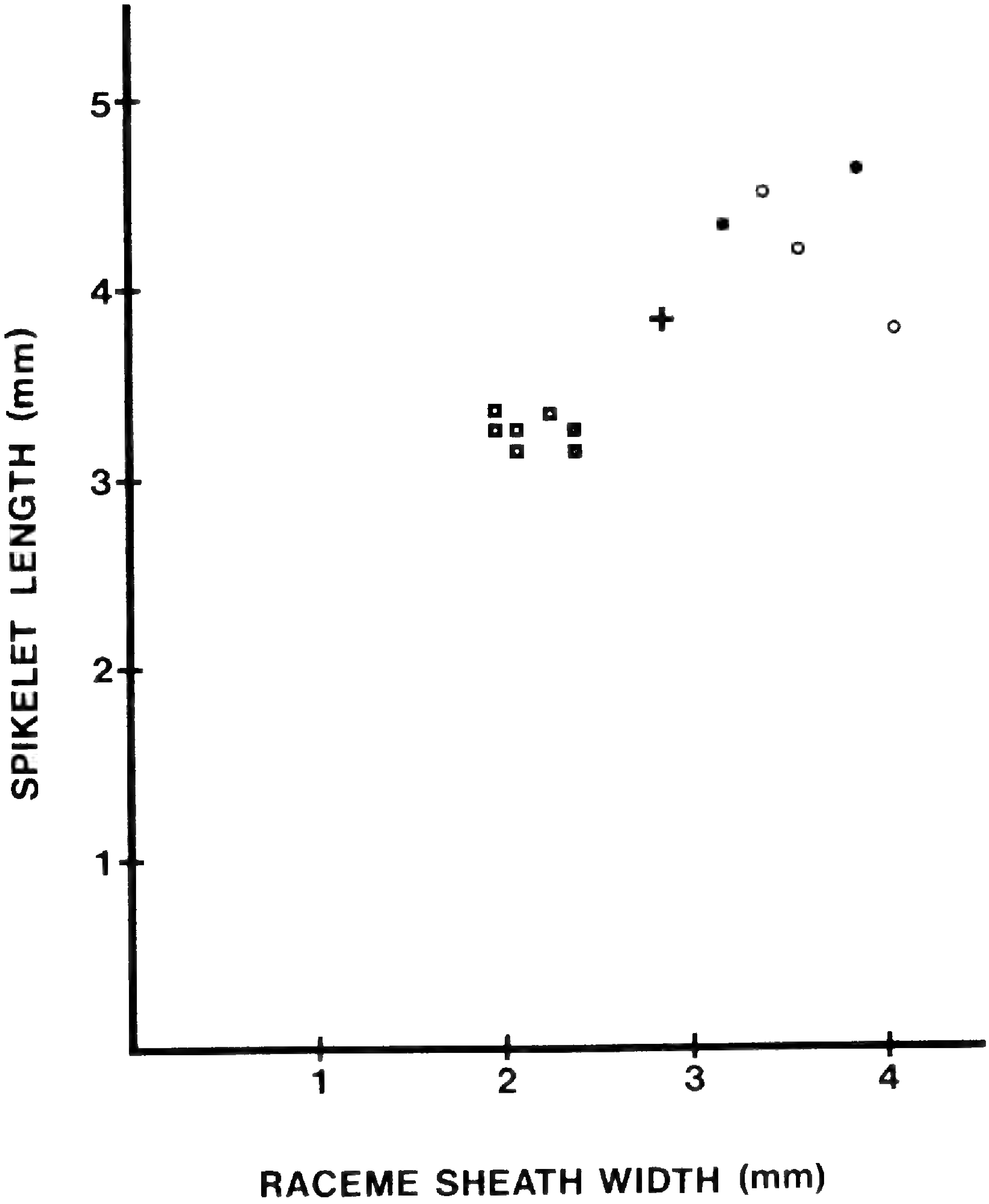


FIGURE 28. Graph of spikelet length vs. raceme-sheath length for seven populations each of robust variant of *Andropogon glomeratus* var. *pumilus* (squares) and *A. longiberbis* (circles; darkened circles indicate two populations with identical values), and for six putative hybrid individuals represented by *Campbell 4266*, Lake County, Florida (cross). Each symbol shows mean of four or five parent plants or six hybrids. Value for each individual is mean of ten measurements of spikelets and raceme sheaths.

pubescence orientation, leaf-blade length and width, number of inflorescence units per stem, raceme-sheath width, peduncle length, spikelet length, callus-hair length, and spikelet-keel scabrousness. Two of the best characters for distinguishing the two parent taxa are raceme-sheath width and spikelet length (FIGURE 28). Variation in these characters for the two parents and the six putative hybrids has been analyzed using discriminant functions (Campbell, 1982a). The six putative hybrids are relatively much less fertile than either parent.

I have observed only two barriers to gene flow in the virginicus complex: cleistogamy and, less importantly, nonsynchronous flowering. Interspecific pollen-style incompatibility, in need of further study, may also contribute to reproductive isolation.

MORPHOLOGY IN RELATION TO TAXONOMY

TABLE 4, which contains information concerning the taxonomically useful variation in the virginicus complex, replaces separate descriptions for the taxa. This format facilitates comparisons between the character states of different taxa and may be used as a multiple-entry key. An explanation of the measurements and abbreviations used is presented in the "Character States" section on pages 194–199.

The first 11 of the 33 characters listed in TABLE 4 pertain to vegetative parts of the plants. Stem height and leaf-blade dimensions vary together and divide the virginicus complex into three rough groups: *Andropogon glomeratus* and *A. floridanus* have the largest dimensions for these characters; *A. gyrans, A. tracyi,* and *A. liebmannii* var. *liebmannii* have the smallest; the rest are mostly intermediate. Because of the overlap between many of the taxa for these characters, they are secondary in importance. Much of the overlap is apparently due to phenotypic response to varying levels of soil moisture and nutrients.

The glaucousness of the leaves and stem internodes of certain taxa is due to a wax that can be rubbed off. It is most conspicuous on young, fresh material. Glaucousness of the leaf is a more reliable character than that of the stem, and it distinguishes both *Andropogon glomeratus* var. *glaucopsis* and *A. virginicus* var. *glaucus* from all other taxa. Infrequently, the leaves of the smooth variant of *A. virginicus* var. *virginicus* are somewhat glaucous.

Variability in the amount and distribution of two types of trichomes is taxonomically useful. The first type is the macroscopic, unicellular hair found on the leaves, below the raceme sheaths, and in the racemes. In this work "pubescence" refers to these hairs. Glabrous leaves lack such hairs. Generally the best place to find pubescence on leaves that are sparsely hairy is near the collar. Glaucous leaves are generally glabrous. Leaf pubescence may disappear as the foliage ages and may also become more appressed. It is therefore best to examine young leaves when trying to determine whether pubescence is spreading or appressed.

The second type of trichome is the microscopic prickle hair; these hairs are usually directed apically on the leaves and keels of the lower glume of the spikelets. When sufficiently abundant, as in plants of *Andropogon glomeratus* (FIGURE 7) and *A. floridanus,* they make the stem sheath scabrous. Pressing the stem sheath firmly with the tip of the finger and moving the finger down the sheath will indicate the absence or the sandpapery effect of the presence of these prickles. They are generally best developed near the collar.

The length of the ligule and its marginal ciliations (FIGURE 4) and the color of the ligule are useful characters; they separate most of *Andropogon glomeratus* from the remainder of the virginicus complex. Previous authors have noted the characteristically long ligules of *A. gyrans* var. *stenophyllus.*

Inflorescence shape is the most conspicuous character of the broomsedges. Since there is considerable variation in this character, authors of earlier works have focused on it and have been confused by the taxa with similar shapes. For example, the range of inflorescence shapes of the robust variant of *Andropogon glomeratus* var. *pumilus* (FIGURE 51) includes those of the rest of *A. glomeratus, A. floridanus* (FIGURE 40), and parts of *A. virginicus* (FIGURES 42, 45) and *A. longiberbis* (FIGURE 41). The similarity of inflorescence shape in *A. glomeratus* and *A. virginicus* is one important factor in the union of the two species by recent American authors (see TABLE 1).

Andropogon brachystachyus and sometimes the drylands variant of *A. virginicus* var. *glaucus* produce long inflorescence branches that spread away from the main stem in smooth arches (FIGURES 24, 43, 44), allowing ready distinction of these plants in the field. Herbarium specimens of these two taxa tend to have rather open inflorescences.

Characters 14 and 15 are attempts to quantify the denseness of the inflorescence. Order of branching refers to the number of rebranchings. For example, FIGURE 10 depicts third-order branching (i.e., three branches at the stem node). These two characters and the number of inflorescence units per stem divide the virginicus complex into three groups that correspond roughly with the groups based on vegetative size. Like stem height and leaf-blade dimensions, they often reflect the suitability of a particular individual's growing conditions. Most of the remaining characters vary independently of stem and leaf dimensions, inflorescence density, and environmental conditions.

Categories of pubescence density below the raceme sheath are shown in FIGURE 3. Seven of the 20 taxa express more than half of the states for this character. There is no overlap in character states in only 25 of the 190 different pairwise combinations of taxa.

The location of the raceme sheath is unique in the common variant of *Andropogon gyrans* var. *gyrans.* Toward the apex of the stem, the internodes are shortened and the stem sheaths become inflated and strongly overlapping. The inflorescence units remain mostly concealed within these inflated stem sheaths. Even though some of the peduncles may elongate and expose the racemes, their subtending raceme sheaths are rarely visible until senescence (FIGURES 29, 30).

Raceme-sheath dimensions, particularly the width, are very useful in distinguishing many of the taxa because of nonoverlapping ranges of mean low and high measurement values.

Peduncle length, spikelet length and width, anther length, and mean percent chasmogamy reflect flowering mode. Mostly chasmogamous plants have long peduncles, large spikelets, and large anthers that are not marcescent at the apex of the fruit within the spikelet (Campbell, 1982b). Plants with predominantly cleistogamous flowers have short peduncles and smaller spikelets and stamens, and the anthers are usually marcescent within the spikelets (see below).

Raceme number distinguishes *Andropogon liebmannii* and is often helpful

TABLE 4. **Character states.**

Character number:		1	2	3	4
		Stem		Leaf	
Taxon	Sample size	height (m.)	glaucousness	glaucousness	pubescence amount
ARCT	17 (8)	(0.9) 1.3 (1.7)	0 (1)	0	0 to D
GYRA	68 (28)	(0.3) 0.8 (1.4)	(0) 1 (2)	0	0 to D
GYRA	37 (17)	(0.5) 0.8 (1.4)	(0) 1 (2)	0	0 to D
comm	23 (10)	(0.5) 0.8 (1.4)	(0) 1	0	0 to D
tenu	14 (7)	(0.5) 0.8 (1.0)	(0) 1 (2)	0	0 to S
STEN	31 (11)	(0.3) 0.7 (1.0)	0,1 (2)	0	0 (S)
TRAC	13 (7)	(0.5) 0.8 (1.2)	0,1	0	0 to S
LIEB	12 (11)	(0.2) 0.9 (1.7)	0	0	S to D
LIEB	6 (5)	(0.2) 0.6 (0.9)	0	0	S to D
PUNG	6 (6)	(0.8) 1.2 (1.7)	0	0	M to D
FLOR	18 (8)	(0.7) 1.4 (2.1)	0 (1)	0	0 (S)
LONG	38 (13)	(0.5) 0.9 (1.5)	0,1	0	S to D
VIRG	147 (75)	(0.4) 1.2 (2.1)	0,1,2	0,1	0 to D
VIRG	98 (43)	(0.4) 1.2 (2.1)	0,1,2	0,1	0 to D
oldf	61 (26)	(0.4) 1.2 (2.1)	0,1	0	S to D
dece	19 (10)	(0.7) 1.2 (1.7)	0	0	S to M
smoo	18 (7)	(0.9) 1.4 (1.8)	2	0,1	0
GLAU	49 (32)	(0.6) 1.2 (1.8)	2	1	0
dryl	20 (15)	(0.7) 1.2 (1.8)	2	1	0
wetl	29 (17)	(0.6) 1.2 (1.7)	2	1	0
BRAC	11 (7)	(1.1) 1.9 (3.1)	0	0	S
GLOM	111 (63)	(0.6) 1.3 (2.5)	0 (2)	0,1	0 to D
GLOM	25 (10)	(0.6) 1.0 (1.6)	0	0	(0) S to D
HIRS	25 (16)	(1.0) 1.4 (2.0)	0	0	(0) S to D
GLAP	22 (13)	(1.2) 1.6 (2.2)	2	1	0 (S)
PUMI	39 (24)	(0.2) 1.4 (2.5)	0	0	0 to D
robu	24 (14)	(0.2) 1.4 (2.5)	0	0	(0) S to D
sout	15 (10)	(0.8) 1.2 (1.5)	0	0	0 to S

in separating the old-field and smooth variants of *A. virginicus* var. *virginicus* from the rest of the virginicus complex. The racemes of the drylands variant of *A. virginicus* var. *glaucus,* the deceptive variant of *A. virginicus* var. *virginicus, A. brachystachyus,* and *A. glomeratus* var. *glaucopsis* are shorter than those of other taxa.

The remaining characters pertain to structures of the dispersal unit. The rachis internodes of *Andropogon floridanus* are uniformly pubescent for their full length and do not become glabrous toward the base, as in other taxa. The

TABLE 4. **Character states** (*continued*).

	5	6	7	8
			Leaf Blade	
Taxon	Leaf pubescence orientation	Sheath scabrousness	length (cm.)	width (mm.)
ARCT	A,S	0	(15) 21 (35)	(3.0) 4.5 (8.0)
GYRA	S (A)	0	(6) 18 (48)	(0.8) 2.2 (5.0)
GYRA	S (A)	0	(8) 20 (48)	(1.4) 2.3 (5.0)
comm	S (A)	0	(8) 20 (48)	(1.4) 2.6 (5.0)
tenu	S	0	(11) 21 (30)	(1.5) 2.0 (3.0)
STEN	S	0	(6) 11 (28)	(0.8) 1.8 (3.0)
TRAC	S	0	(10) 16 (22)	(1.2) 1.9 (2.6)
LIEB	S	0 (1)	(3) 16 (35)	(2.5) 4.4 (7.5)
LIEB	S	0 (1)	(3) 8 (15)	(2.5) 4.2 (6.5)
PUNG	S	0	(15) 24 (35)	(2.5) 4.6 (7.5)
FLOR	S	0,1	(32) 42 (61)	(2.9) 3.8 (5.0)
LONG	A (S)	0	(11) 26 (50)	(2.0) 3.2 (5.5)
VIRG	S	0 (1)	(11) 25 (52)	(1.7) 3.6 (6.5)
VIRG	S	0 (1)	(11) 28 (52)	(1.7) 3.3 (5.5)
oldf	S	0 (1)	(11) 30 (52)	(1.7) 3.0 (5.0)
dece	S	0	(15) 24 (35)	(2.5) 3.6 (5.5)
smoo	-	0	(22) 27 (38)	(2.3) 3.5 (5.0)
GLAU	-	0	(12) 19 (38)	(2.0) 4.3 (6.5)
dryl	-	0	(12) 17 (27)	(2.0) 3.5 (5.0)
wetl	-	0	(13) 20 (38)	(2.6) 4.9 (6.5)
BRAC	S	0	(21) 33 (54)	(2.3) 3.7 (6.0)
GLOM	S (A)	1 (0)	(13) 41 (109)	(2.9) 4.8 (9.5)
GLOM	S	1	(16) 37 (55)	(2.8) 4.3 (7.5)
HIRS	S	1 (0)	(24) 41 (60)	(2.0) 4.2 (6.0)
GLAP	S	0 (1)	(33) 40 (75)	(3.0) 5.0 (7.0)
PUMI	S (A)	0,1	(13) 44 (109)	(3.0) 5.4 (9.5)
robu	S (A)	0,1	(13) 46 (109)	(3.0) 6.0 (9.5)
sout	S	1	(30) 41 (66)	(3.5) 4.4 (6.0)

length of the callus hairs is positively correlated with the general density of hairs on all parts of the dispersal unit. *Andropogon gyrans* and *A. longiberbis*, with callus hairs often to 5 mm long, have more densely pubescent rachis internodes and pedicels than all other taxa except *A. floridanus*. The keels of the lower glumes of the spikelets bear prickles that often extend below the middle of the glume in *A. arctatus* and *A. glomeratus* var. *pumilus*. The awn of the fertile lemma is more or less twisted where it joins the lemma and is relatively short in *A. arctatus*, *A. floridanus*, and *A. brachystachyus*. Variation

TABLE 4. **Character states** (*continued*).

	9	10	11
	Ligule		
Taxon	length (mm.)	ciliation length (mm.)	color
ARCT	(0.3) 0.6 (0.9)	0-0.5	Brown
GYRA	(0.3) 0.9 (1.5)	0-0.7	Light brown (brown)
GYRA	(0.3) 0.6 (1.1)	0-0.3	Light brown to brown
comm	(0.3) 0.6 (1.1)	0-0.7	Light brown
tenu	(0.4) 0.6 (0.8)	0-0.3	Light brown to brown
STEN	(0.8) 1.1 (1.5)	0-0.1	Light brown
TRAC	(0.2) 0.4 (0.5)	0.2-0.8	Brown
LIEB	(0.5) 0.8 (1.2)	0-0.4	Whitish to light brown
LIEB	(0.5) 0.7 (1.9)	0-0.2	Whitish to light brown
PUNG	(0.7) 0.9 (1.2)	0-0.4	Whitish to light brown
FLOR	(0.4) 0.7 (1.2)	0.2-1.3	Brown
LONG	(0.2) 0.4 (0.6)	0.3-0.6	Light brown to brown
VIRG	(0.2) 0.5 (1.0)	0.2-1.3	Brown (light brown)
VIRG	(0.2) 0.5 (1.0)	0.2-1.3	Brown (light brown)
oldf	(0.2) 0.5 (0.8)	0.2-1.3	Brown
dece	(0.3) 0.5 (0.7)	0.5-1.1	Brown
smoo	(0.4) 0.6 (1.0)	0.3-0.9	Brown (light brown)
GLAU	(0.2) 0.4 (0.5)	0.3-1.2	Brown
dryl	(0.2) 0.3 (0.5)	0.4-1.2	Brown
wetl	(0.2) 0.4 (0.5)	0.3-0.8	Brown
BRAC	(0.2) 0.4 (0.5)	0.6-1.5	Brown
GLOM	(0.6) 1.2 (2.2)	0-0.9	Whitish (brown)
GLOM	(1.0) 1.2 (2.0)	0-0.3	Whitish to light brown
HIRS	(0.7) 1.2 (2.0)	0-0.3	Whitish to light brown
GLAP	(0.9) 1.5 (2.0)	0-0.2	Whitish to light brown
PUMI	(0.6) 1.1 (2.2)	0.2-0.9	Light brown to brown
robu	(0.6) 0.8 (1.3)	0.2-0.9	Light brown to brown
sout	(1.0) 1.5 (2.2)	0.2-0.5	Light brown

in anther length and the marcescence of the anther are discussed in the following section.

The fruits are oblong to linear and are usually 2–3 mm long. Their size varies sufficiently with environmental conditions so as to be of little taxonomic value.

CHARACTER STATES

The measurements in TABLE 4 are based on herbarium specimens (primarily those of the author) and field observations covering the taxonomically useful

TABLE 4. **Character states** (*continued*).

	12	13	14	15	16
	Inflorescence				
Taxon	shape	orientation of branches	maximum branching	maximum branches	units/stem
ARCT	Oblong to ovate	Erect	1-3	1-5	(5) 16 (45)
GYRA	Linear to ovate	Erect	1-2	1-5	(2) 9 (31)
GYRA	Linear to ovate	Erect	1-2	1-5	(3) 9 (31)
comm	Linear to ovate	Erect	1-2	2-5	(3) 12 (31)
tenu	Linear	Erect	1-2	1-3	(3) 8 (13)
STEN	Linear	Erect	1-2	1-3	(2) 11 (26)
TRAC	Linear	Erect	1-2	1-2	(3) 8 (11)
LIEB	Linear to oblong	Erect	1-3	2-3	(1) 16 (50)
LIEB	Linear	Erect	1 (2)	1-2	(1) 4 (7)
PUNG	Linear to oblong	Erect	2-3	2-3	(7) 27 (50)
FLOR	Obla to obovate	Erect	2-3	2-5	(9) 51 (210)
LONG	Linear to oblong	Erect	2-3	2-4	(7) 45 (97)
VIRG	Linear to obpy	Erect or arching	2-4	2-6	(6) 62 (195)
VIRG	Linear to oblong	Erect	2-4	2-5	(6) 55 (175)
oldf	Linear to oblong	Erect	2-3	2-5	(6) 51 (150)
dece	Linear to oblong	Erect (arching)	2-4	2-4	(20) 82 (175)
smoo	Linear to obla	Erect	2-3	2-3	(12) 28 (60)
GLAU	Linear to obpy	Erect or arching	2-3	2-6	(19) 78 (190)
dryl	Linear to obpy	Erect or arching	2-3	2-3	(31) 84 (190)
wetl	Linear to oblong	Erect	2-3	2-6	(19) 72 (113)
BRAC	Ovate to obpy	Arching	2-3	3-5	(12) 75 (190)
GLOM	(Linear to) obpy	Erect	2-5	3-11	(10) 123 (600)
GLOM	Oblo to obpy	Erect	2-4	3-4	(25) 107 (200)
HIRS	(Linear to) oblong	Erect	2-4	4-5	(10) 96 (205)
GLAP	(Linear to) oblong	Erect	3-4	4-5	(30) 159 (400)
PUMI	Obla to obpy	Erect	2-5	3-11	(15) 132 (600)
robu	Obla to obpy	Erect	3-5	3-11	(28) 169 (600)
sout	Obla to obpy	Erect	2-3	3-7	(15) 95 (200)

morphological variation and the geographic range of the taxa. The sample size reflects the complexity of the taxa or (with *Andropogon liebmannii* var. *liebmannii* and the tenuous variant of *A. gyrans* var. *gyrans*) a low frequency of occurrence in nature. The first number for sample size in TABLE 4 is the total number of plants measured; the number of populations included in the measurements is in parentheses. For some taxa many plants have been measured for certain critical characters and fewer plants for other characters less important in distinguishing the taxa. Also, numerous herbarium specimens have been spot checked for many of the characters. For all quantitative measurements,

TABLE 4. **Character states** (*continued*).

	17	18	19	20
	Pubescence below raceme	Raceme Sheath		
Taxon	sheath	location	length (cm.)	width (mm.)
ARCT	0 to D	0	(3.3) 3.8-6.8 (9.0)	(2.5) 3.2-4.0 (5.0)
GYRA	0 to D	0,1	(3.5) 4.6-6.9 (13.5)	(1.5) 2.7-4.7 (8.0)
GYRA	0 to D	0,1	(3.5) 4.6-7.0 (13.5)	(1.5) 2.8-4.7 (8.0)
comm	(0 to) D	1 (0)	(3.5) 4.4-5.5 (13.5)	(2.0) 3.1-5.1 (8.0)
tenu	S to D	0	(4.0) 4.9-7.9 (9.5)	(1.5) 2.5-4.3 (5.0)
STEN	0 to D	0	(2.6) 4.2-6.6 (8.5)	(2.0) 2.8-4.8 (6.3)
TRAC	0 to D	0	(2.8) 4.1-5.8 (7.2)	(3.0) 4.0-4.7 (5.8)
LIEB	0 to D	0	(4.0) 4.9-7.4 (10.0)	(3.0) 4.2-6.1 (10.1)
LIEB	0 to S	0	(4.2) 4.7-7.0 (7.5)	(3.0) 3.2-4.2 (4.5)
PUNG	M to D	0	(4.0) 5.1-7.8 (10.0)	(4.1) 5.3-8.0 (10.1)
FLOR	0 to D	0	(3.0) 4.0-5.9 (7.0)	(1.5) 2.0-2.7 (3.6)
LONG	S to D	0	(2.5) 3.0-4.5 (6.0)	(2.5) 3.2-4.1 (5.5)
VIRG	0 to D	0	(2.1) 3.1-4.6 (6.7)	(1.7) 3.0-3.8 (5.6)
VIRG	0 to M	0	(2.2) 3.2-4.8 (6.7)	(1.7) 3.0-3.8 (5.6)
oldf	0 to S (M)	0	(2.3) 3.4-5.2 (6.7)	(2.2) 3.3-4.4 (5.6)
dece	(0) S to M	0	(2.2) 2.5-3.8 (4.5)	(1.7) 2.4-3.1 (4.0)
smoo	0 (S)	0	(2.8) 3.3-4.7 (6.7)	(3.0) 3.2-3.8 (5.2)
GLAU	0 to D	0	(2.1) 2.9-4.3 (6.0)	(2.7) 3.1-3.8 (5.5)
dryl	0	0	(2.1) 2.6-3.8 (4.9)	(2.7) 3.0-3.5 (4.5)
wetl	S to D	0	(2.4) 3.2-4.8 (6.0)	(2.7) 3.2-4.2 (5.5)
BRAC	(0 to) M	0	(2.1) 2.4-3.5 (4.1)	(2.3) 2.6-3.0 (3.8)
GLOM	S to D	0	(2.0) 2.9-4.4 (6.5)	(1.3) 2.3-3.1 (4.7)
GLOM	S to D	0	(2.5) 3.4-5.2 (6.5)	(2.0) 2.5-3.4 (4.7)
HIRS	(S) M to D	0	(2.5) 2.9-4.6 (5.7)	(2.0) 2.4-3.1 (4.0)
GLAP	(S) M to D	0	(2.0) 2.4-3.6 (4.4)	(1.3) 2.0-2.5 (3.0)
PUMI	S to D	0	(2.0) 2.9-4.4 (6.3)	(1.5) 2.1-2.9 (4.4)
robu	(S) M to D	0	(2.0) 2.9-4.3 (5.2)	(1.5) 2.0-2.5 (3.0)
sout	S to M	0	(2.3) 2.9-4.5 (6.3)	(1.5) 2.3-3.3 (4.4)

if two numbers are provided (characters 10, 14, 15, 22, 26, and 27) they represent the range of values recorded. Where three numbers are given (characters 1, 7–9, 16, 29, and 31), the first and last, which are enclosed in parentheses, indicate the range around the mean value. For four numbers (characters 19–21, 23, and 25) the first and last again indicate the range, while the two middle values represent the mean of the smallest and largest values recorded for all the plants. For all other characters, states enclosed in parentheses rarely occur in the taxon. If two states are given, they are both of intermediate

TABLE 4. **Character states** (*continued*).

	21	22	23
	Peduncle	Raceme	
Taxon	length (mm.)	number	length (cm.)
ARCT	(9) 26-66 (115)	2 (3, 4)	(2.2) 2.6-4.3 (5.3)
GYRA	(1) 5-31 (195)	2-5	(1.5) 2.8-4.2 (5.5)
GYRA	(1) 5-42 (195)	2-5	(1.5) 2.6-3.9 (5.5)
comm	(4) 6-60 (195)	2-5	(1.5) 2.5-3.7 (5.5)
tenu	(1) 5-25 (50)	2-4	(2.3) 2.7-4.2 (5.5)
STEN	(3) 4-16 (45)	2 (3)	(2.5) 4.0-4.5 (6.0)
TRAC	(9) 14-31 (65)	2	(1.5) 2.4-3.6 (4.2)
LIEB	(10) 24-68 (130)	2-13	(2.0) 2.4-4.0 (5.0)
LIEB	(20) 32-88 (130)	2-9	(2.0) 2.5-4.1 (5.0)
PUNG	(10) 15-47 (70)	2-13	(2.0) 2.3-3.9 (4.7)
FLOR	(10) 19-48 (93)	2 (-4)	(2.0) 2.5-3.7 (4.5)
LONG	(1) 3-4 (13)	2 (3)	(1.3) 1.8-2.6 (4.0)
VIRG	(1) 4-6 (30)	2-7	(0.5) 1.7-2.8 (4.4)
VIRG	(1) 4-6 (30)	2-7	(0.5) 1.7-3.0 (4.4)
oldf	(2) 4-6 (12)	2-5 (-7)	(0.5) 1.9-3.3 (4.4)
dece	(1) 4-9 (30)	2 (3)	(1.3) 1.5-2.3 (3.0)
smoo	(2) 3-4 (6)	2-4 (-7)	(1.1) 1.5-2.9 (3.6)
GLAU	(2) 3-4 (10)	2 (3)	(1.4) 1.8-2.7 (4.0)
dryl	(2) 3-4 (5)	2	(1.4) 1.7-2.4 (3.2)
wetl	(2) 3-5 (10)	2 (3)	(1.5) 2.0-3.0 (4.0)
BRAC	(13) 20-31 (43)	2 (3)	(1.2) 1.5-2.1 (2.6)
GLOM	(1) 6-14 (60)	2 (-4)	(1.0) 1.7-2.5 (3.5)
GLOM	(4) 11-35 (60)	2 (-4)	(1.5) 2.1-2.9 (3.5)
HIRS	(2) 3-5 (8)	2	(1.3) 1.7-2.8 (3.3)
GLAP	(1) 2-4 (6)	2	(1.0) 1.3-2.0 (2.3)
PUMI	(2) 7-13 (40)	2 (-4)	(1.3) 1.8-2.4 (3.0)
robu	(2) 8-15 (40)	2	(1.3) 1.7-2.5 (3.0)
sout	(2) 5-10 (16)	2 (-4)	(1.7) 1.9-2.3 (2.8)

frequency (or both rare if in parentheses). For glaucousness (characters 2 and 3) "0" means absence and "1" presence. For stem glaucousness "1" further means that the glaucousness does not occur in the internode below about 2 cm under the node, and "2" indicates general occurrence of glaucousness in the internode. Absence or presence of sheath scabrousness (character 6) is shown with a "0" or a "1." In the pubescence-density characters (4 and 17) "0" is absence, "S" sparse, "M" moderate, and "D" dense. Pubescence orientation (character 5) is either appressed ("A"), spreading ("S"), or a combination of the two; when the leaves are always glabrous, this character is left blank.

TABLE 4. **Character states** (*continued*).

	24	25	26
Taxon	Rachis internode pubescence	Spikelet length (mm.)	width (mm.)
ARCT	0,1	(4.3) 4.9-5.4 (6.1)	0.7-1.0
GYRA	0	(3.0) 3.9-4.7 (5.7)	0.5-0.7
GYRA	0	(3.5) 4.1-4.5 (5.7)	0.5-0.7
comm	0	(3.5) 4.2-4.5 (5.7)	0.5-0.7
tenu	0	(3.5) 4.0-4.5 (5.2)	0.5-0.6
STEN	0	(3.0) 3.4-5.1 (5.5)	0.5-0.6
TRAC	0	(4.0) 4.8-5.0 (5.5)	0.6-0.8
LIEB	0	(3.0) 4.0-4.5 (6.0)	0.5-1.0
LIEB	0	(3.0) 3.4-3.9 (4.2)	0.5-0.9
PUNG	0	(4.3) 4.7-5.1 (6.9)	0.7-1.0
FLOR	1	(3.8) 4.4-4.8 (5.5)	0.5-0.7
LONG	0	(3.5) 4.1-4.5 (5.0)	0.5-0.8
VIRG	0	(2.6) 3.5-3.8 (4.7)	0.4-0.6
VIRG	0	(2.9) 3.5-3.8 (4.7)	0.4-0.6
oldf	0	(2.9) 3.7-3.9 (4.7)	0.4-0.6
dece	0	(3.0) 3.3-3.6 (4.0)	0.4-0.6
smoo	0	(3.0) 3.5-3.7 (4.2)	0.4-0.6
GLAU	0	(2.6) 3.4-3.7 (4.4)	0.4-0.5
dryl	0	(2.6) 3.2-3.5 (3.9)	0.4-0.5
wetl	0	(3.0) 3.5-3.9 (4.9)	0.4-0.5
BRAC	0	(4.1) 4.4-4.6 (5.0)	0.5-0.7
GLOM	0	(3.0) 3.7-4.0 (5.0)	0.4-0.6
GLOM	0	(3.8) 4.1-4.4 (5.0)	0.5-0.6
HIRS	0	(3.4) 3.6-3.8 (4.6)	0.4-0.6
GLAP	0	(3.0) 3.2-3.5 (3.8)	0.4-0.6
PUMI	0	(3.0) 3.8-4.1 (5.0)	0.4-0.6
robu	0	(3.0) 3.4-3.8 (4.5)	0.4-0.6
sout	0	(3.5) 4.2-4.5 (5.0)	0.4-0.6

Inflorescence shape (character 12) is linear, oblanceolate (abbreviated "obla"), oblong, ovate, obovate, or obpyramidal (abbreviated "obpy"). Raceme sheaths are located (character 18) so as to be either largely exposed ("0") or mostly hidden within enlarged stem sheaths ("1") after anthesis. Pubescence on the rachis internode (character 24) is either relatively sparse toward the base of the internode ("0") or uniformly distributed along the internode ("1"). Lower glume scabrousness (character 28) either occurs only above the middle of the glume ("0") or extends below the middle ("1"). Percent chasmogamy (character

TABLE 4. **Character states** (*continued*).

	27	28	29	30
			Awn	
Taxon	Maximum callus hair length (mm.)	Lower glume keel scabrousness	length (mm.)	base
ARCT	1.5-2.5	1	(0.5) 0.8 (1.6)	(0) 1
GYRA	1-5	0	(0.8) 1.8 (2.4)	0,1
GYRA	2-5	0	(1.3) 1.5 (2.2)	0,1
comm	2.5-4	0	(1.3) 1.8 (2.3)	(0) 1
tenu	2-5	0	(1.3) 2.0 (2.4)	(0) 1
STEN	1-2.5	0	(0.8) 1.5 (2.2)	0,1
TRAC	1.5-3.5	0	(1.1) 1.5 (2.3)	0,1
LIEB	1.5-2	0,1	(1.2) 1.8 (2.4)	1
LIEB	1.5-2	0	(1.2) 1.4 (1.6)	1
PUNG	1.5-2	0,1	(1.7) 2.1 (2.4)	1
FLOR	1-3	0	(0.5) 0.9 (1.5)	0
LONG	1.5-5	0	(1.0) 1.6 (2.1)	0,1
VIRG	1-3	0 (1)	(0.6) 1.4 (2.1)	0 (1)
VIRG	1-2.5	0 (1)	(0.8) 1.4 (2.0)	0
oldf	1-2.5	0 (1)	(1.0) 1.5 (2.0)	0
dece	1-2.5	0	(0.8) 1.2 (1.7)	0
smoo	1-1.5	0 (1)	(1.2) 1.5 (1.8)	0
GLAU	1-3	0	(0.6) 1.2 (2.1)	0 (1)
dryl	1-3	0	(0.6) 1.1 (1.5)	0 (1)
wetl	1-2.5	0	(0.9) 1.4 (2.1)	0 (1)
BRAC	1-1.5	0	(0.2) 0.7 (1.1)	0
GLOM	1-2.5	0,1	(0.6) 1.3 (1.9)	0 (1)
GLOM	1.5-2.5	0 (1)	(0.8) 1.2 (1.8)	1
HIRS	1-2	0 (1)	(1.0) 1.4 (1.7)	(0) 1
GLAP	1-2	0 (1)	(0.9) 1.2 (1.6)	(0) 1
PUMI	1-2.5	1	(0.6) 1.2 (1.9)	(0) 1
robu	1.5-2.5	1	(0.9) 1.4 (1.9)	(0) 1
sout	1-2	1	(0.6) 1.1 (1.7)	1

33), given as the mean (one standard error), is determined by looking for the presence (cleistogamy) or absence (chasmogamy) of a marcescent anther and stigmas in at least 30 postanthesis spikelets per plant.

TAXONOMIC TREATMENT

Taxonomic rank within the complex is based primarily on morphological distance between the taxa. Distances between the taxa have been determined

TABLE 4. **Character states** (*continued*).

	31	32	33
	Anther		
Taxon	length (mm.)	color	Mean percent chasmogamy ± S.E.
ARCT	(2.0) 2.5 (3.3)	Red	100 ± 0
GYRA	(0.6) 1.1 (1.4)	Yellow or purple	38 ± 3.3
GYRA	(0.7) 1.1 (1.4)	Yellow or purple	36 ± 4.7
comm	(0.9) 1.2 (1.4)	Yellow (purple)	38 ± 6.1
tenu	(0.7) 0.9 (1.2)	Yellow or purple	34 ± 5.2
STEN	(0.6) 1.2 (1.7)	Yellow	40 ± 6.5
TRAC	(1.2) 1.5 (2.0)	Yellow	98 ± 0.2
LIEB	(0.7) 1.2 (1.4)	Yellow	95 ± 1.2
LIEB	(1.1) 1.2 (1.4)	Yellow	98 ± 0.7
PUNG	(0.7) 1.1 (1.4)	Yellow	91 ± 2.2
FLOR	(1.3) 1.5 (2.0)	Yellow (purple)	98 ± 0.7
LONG	(0.9) 1.2 (1.6)	Yellow	84 ± 3.4
VIRG	(0.6) 0.9 (1.5)	Yellow or purple	64 ± 2.8
VIRG	(0.6) 0.8 (1.5)	Yellow or purple	60 ± 2.9
oldf	(0.6) 0.9 (1.2)	Yellow or purple	47 ± 5.9
dece	(0.6) 1.0 (1.5)	Yellow	88 ± 3.6
smoo	(0.6) 0.7 (1.0)	Purple	44 ± 4.8
GLAU	(0.7) 1.0 (1.2)	Yellow	70 ± 1.5
dryl	(0.9) 1.0 (1.5)	Yellow	97 ± 0.9
wetl	(0.7) 0.9 (1.1)	Yellow	42 ± 2.3
BRAC	(1.7) 2.1 (2.4)	Red	99 ± 0.01
GLOM	(0.5) 0.9 (1.5)	Yellow, red, or purple	66 ± 1.6
GLOM	(0.9) 1.2 (1.5)	Yellow	79 ± 3.4
HIRS	(0.7) 0.8 (1.1)	Yellow or purple	41 ± 3.2
GLAP	(0.5) 0.7 (0.9)	Yellow or purple	25 ± 2.9
PUMI	(0.7) 0.9 (1.1)	Yellow	93 ± 0.9
robu	(0.7) 0.9 (1.1)	Yellow	96 ± 0.6
sout	(0.8) 0.9 (1.0)	--	88 ± 1.9

through comparisons of the 33 characters (see TABLE 4) used in this study, assigning a value of “0” for no difference, “½” for intermediate overlap, and “1” for little or no overlap between the character states. (The rules for determining these values for each of the characters are presented in APPENDIX B.) The sum of these values for all the characters for any single pair of taxa is the distance between them (TABLES 5, 6). This distance represents the probability of misidentifying a specimen of one taxon as another taxon. The maximum distance between any pair of taxa is 21.5 (*Andropogon tracyi* and *A. glomeratus* var. *glaucopsis*), and the minimum between any of the lowest-ranking taxa

TABLE 5. **Morphological distance between the species.***

	ARCT	GYRA	TRAC	LIEB	FLOR	LONG	VIRG	BRAC	GLOM
ARCT									
GYRA	11								
TRAC	10	8							
LIEB	8	7	9.5						
FLOR	11.5	13	10.5	12					
LONG	11.5	7.5	9	12	12				
VIRG	12	9.5	12	12	9.5	6.5			
BRAC	13	17	16	17	9.5	14	9.5		
GLOM	15	13.5	14.5	12	10	12	8	13.5	

*For an explanation of how these distance values are determined, see the section on taxonomic rank and APPENDIX B.

(i.e., those that are not polytypic) is 3 (the old-field and smooth variants of *A. virginicus* var. *virginicus*). Any distance less than 6 is found only within species, and any greater than 9 occurs only between species.

In six of the thirty-six species pairs (TABLE 5), the distance is less than 9. In all of these cases, one or both of the species is polytypic. The character states of the polytypic taxa are the weighted mean or encompass the full range of variation of the subspecific taxa. This method of deriving character states of the polytypic taxa minimizes their distance from other taxa. The distances from the lowest-ranking taxa of a polytypic species to the lowest-ranking taxa of other species are generally greater than the distances separating the polytypic species (TABLE 6). Hence, in five of the six cases of species-to-species distances less than 9, most distances between the lowest-ranking taxa are at least 9. The one case in which most of the lowest-ranking taxa of the two species are separated by less than 9 is *Andropogon longiberbis* and *A. virginicus.* The reasons for maintaining these taxa as species are given in the discussion of *A. longiberbis.*

Morphological distance usually coincides with differences in ecological preferences or geographic distribution. More closely related taxa (e.g., *Andropogon glomeratus* vars. *hirsutior* and *glaucopsis*) may, however, have very similar ecological preferences and ranges.

"Taxon" is used here for a group of populations with similar morphological characteristics and ecological preferences. Only taxa separated by consistent and appreciable morphological gaps are recognized nomenclaturally. Nine of the taxa, here called variants, are not recognized formally because of the extreme difficulty in distinguishing between those belonging to the same variety. Apart from nomenclatural status, the variants are treated in the same fashion as species and varieties. The taxa are arranged in the taxonomic treatment so as to place those that are most closely related next to one another. Ambiguous names in the virginicus complex are discussed in APPENDIX C.

In the citation of herbarium specimens, abbreviations of the institutions follow the sixth edition of *Index Herbariorum* (Holmgren & Keuken, 1974). The herbaria and their abbreviations are listed in the acknowledgments.

Ordinarily, one specimen per county has been cited for taxa in the United States, and all specimens represented by a dot on the distribution maps have been cited for Mexico, Central America, the West Indies, and South America. Because the old-field variant of *Andropogon virginicus* var. *virginicus* and the robust variant of *A. glomeratus* var. *pumilus* are so abundant, only a representative number of counties from the United States have been cited.

It is important to read the section on morphology in relation to taxonomy before using the keys. All characters concerning the leaves are based on healthy, nonsenescent leaves at the second to fourth nodes above the base of the plant. All characters concerning the dispersal units are based on units near the middle of the raceme.

KEY TO THE SPECIES OF THE VIRGINICUS COMPLEX

1. Postflowering peduncles less than 10 mm long.
    2. Plants small—stems usually less than 1 m tall, leaves usually less than 3 mm wide, inflorescence branching of first or second order only, inflorescence units less than 30 per stem; raceme sheaths usually more than 4.6 cm long. .... 2. *Andropogon gyrans.*
    2. Plants larger—stems usually more than 1 m tall, leaves usually more than 3 mm wide, inflorescence branching of second or higher order, inflorescence units more than 30 per stem; raceme sheaths usually less than 4.6 cm long.
        3. Spikelets more than 4 mm long; leaf pubescence appressed (rarely spreading); longest callus hairs often more than 2.5 mm long. .... 6. *Andropogon longiberbis.*
        3. Spikelets usually less than 4 mm long; leaf pubescence spreading (rarely appressed); longest callus hairs less than 2.5 mm long.
            4. Leaves usually over 37 cm long; stem sheaths often scabrous; ligules usually more than 1 mm long (if less than 1 mm, then keels of lower glume of spikelets often scabrous to below middle). .. 9. *Andropogon glomeratus.*
            4. Leaves usually less than 31 cm long; stem sheaths smooth (very rarely somewhat scabrous); ligules less than 1 mm long; keels of lower glume scabrous only above middle. .... 7. *Andropogon virginicus.*
1. One or more postflowering peduncles more than 15 mm long.
    5. Inflorescence units with (2 to) 4 to 6 (to 13) racemes. .... 4. *Andropogon liebmannii.*
    5. Inflorescence units usually with 2 racemes, occasionally with 3 or more.
        6. Plants small—stems usually less than 1 m tall, leaves usually less than 3 mm wide, inflorescence branching of first or second order only, inflorescence units less than 30 per stem.
            7. Spikelets (4–)4.8–5(–5.5) by 0.6–0.8 mm; racemes in twos; anthers more than 1.2 mm long. .... 3. *Andropogon tracyi.*
            7. Spikelets (3.5–)4–4.5(–5.2) by 0.5–0.6 mm; racemes often more than 2 per inflorescence unit; anthers less than 1.2 mm long. .. 2. *Andropogon gyrans.*
        6. Plants larger—stems usually more than 1 m tall, leaves usually more than 3

TABLE 6. **Morphological distance between the taxa.**

	ARCT	GYRA	GYRA	comm	tenu	STEN	TRAC	LIEB	LIEB	PUNG	FLOR	LONG	VIRG	VIRG	oldf	dece	smoo	GLAU	dryl	wetl	BRAC	GLOM	GLOM	HIRS	GLAP	PUMI	robu	sout
ARCT																												
GYRA	11																											
GYRA	12.*	0																										
comm	11.	2.	1																									
tenu	12.	2	2	4																								
STEN	12	6	5.	5	5																							
TRAC	10	8	7	9.	10	6.																						
LIEB	8	7	7.	8.	9.	6	9.																					
LIEB	11.	8	8.	10	9.	7.	10	4.																				
PUNG	9.	9.	9.	11	11.	10	11	2	9																			
FLOR	11.	13	13.	13.	17.	14	10.	12	16	13																		
LONG	11.	7.	8	8	10.	10	9	12	14.	13.	12																	
VIRG	12	9.	9.	10.	10.	12	12	12	14	13.	9.	6.																
VIRG	13.	8	10	11	9	10	11.	12.	13	14.	9.	6.	1.															
oldf	13	9	11	10.	11	11	11	12	12.	15	11.	7	3.	2														
dece	14	14	14	14	17	11	14.	13.	14.	13	10	6.	4	4	4.													
smoo	15	10	10.	12	13	15	16.	15.	15.	17	12.	11	3	2	3	7.												
GLAU	13.	13.	14	14.	15	11	13	16	17.	17	12.	8	2	2.	5	5	4.											
dryl	15	16	16	16	15	13.	14	17	18.	17	13.	10	3.	5	8.	5.	5.	0.										
wetl	14.	12	13.	12	16	12	12.	16.	18	17.	12.	7.	3.	2.	4	6	4.	1.	4									
BRAC	13	17	17.	19	20.	17	16	17	19.	16.	9.	14	9.	10.	12.	8	14.	12	13	14.								
GLOM	15	13.	14	13.	16	12	14.	12	15.	13	10	12	8	8	11	10.	10	9.	12	10	13.							
GLOM	12	11.	12.	11.	14.	12	14.	8.	13	11	10.	9	10.	9.	11.	9	14	12	14.	12.	13	3						
HIRS	15	13	15.	14	16	14	19.	12.	15.	12.	13.	11	8.	7	9	7.	11.	11.	14.	11	14	3	4					
GLAP	18	17	17	19.	17	15.	21.	16.	19	17.	15.	16.	10	9.	11.	11	11.	10	11.	10.	16	8	9	6.				
PUMI	13	14	14.	14.	16	12.	15.	11.	15.	12	9.	11.	9	9.	12.	8	13	11.	13	11.	12	2	4.	5.	8.			
robu	13	15.	15	14	16.	13.	16	12	13.	11.	10	13	9.	10	12.	8	13	12	13	12	13	4.	6	6.	9	1.		
sout	12	12.	12.	14	15.	12.	16.	13.	17.	14.	11	8.	9	8.	9.	9	12.	11	13.	11.	12	4	5	5	9	4	6	

*The decimal point following a distance value indicates that the value should be increased by 0.5 (e.g., 12. = 12.5).

mm wide, inflorescence branching of second or higher order, inflorescence units more than 30 per stem.

8. Racemes usually less than 2.1(–2.6) cm long; inflorescence branches long and arching, inflorescence open, loose. . . 8. *Andropogon brachystachyus.*
8. Racemes usually longer than 2 cm; inflorescence branches mostly erect, inflorescence more or less dense.
    9. Rachis internodes densely pubescent over entire length; spikelets usually more than 4.4 mm long; awns usually less than 1 cm long; anthers usually more than 1.5 mm long.
        10. Leaves (32–)42(–61) cm long, glabrous; stem sheaths often scabrous; inflorescence units (9 to) 51 (to 210) per stem; anthers less than 2 mm long. 5. *Andropogon floridanus.*
        10. Leaves (15–)21(–35) cm long, often pubescent; stem sheaths smooth; inflorescence units (9 to) 16 (to 45) per stem; anthers more than 2 mm long. . . . . 1. *Andropogon arctatus.*
    9. Rachis internodes sparsely pubescent toward base; spikelets usually less than 4.4 mm long; awns usually more than 1 mm long; anthers less than 1.5 mm long.
        11. Leaves usually over 37 cm long; stem sheaths often scabrous; ligules usually more than 1 mm long (if less than 1 mm, then keels of lower glume of spikelets often scabrous to below middle). . . . . 9. *Andropogon glomeratus.*
        11. Leaves usually less than 31 cm long; stem sheaths smooth (very rarely somewhat scabrous); ligules less than 1 mm long; keels of lower glume scabrous only above middle. . . . . 7. *Andropogon virginicus.*

KEY TO THE TAXA OF THE VIRGINICUS COMPLEX AND ANDROPOGON TERNARIUS

1. Postflowering peduncles less than 10 mm long.
    2. Leaves strongly glaucous, especially when young.
        3. Ligules (0.9–)1.5(–2) mm long, with ciliations less than 0.3 mm long; leaf blades usually more than 35 cm long; racemes (1–)1.3–2(–2.3) cm long; pubescence below raceme sheath moderate to dense. . . . . 9c. *A. glomeratus* var. *glaucopsis.*
        3. Ligules (0.2–)0.4(–0.5) mm long, with ciliations more than 0.3 mm long; leaf blades usually less than 35 cm long; racemes (1.4–)1.8–2.7(–4) cm long (if less than 2 cm, then pubescence below raceme sheath usually absent or sparse).
            4. Pubescence below raceme sheaths absent; raceme sheaths (2.1–)2.6–3.8 (–4.9) cm long; racemes (1.4–)1.7–2.4(–3.2) cm long; spikelets (2.6–)3.4–3.7 (–4.4) mm long; plants of well-drained soils on Coastal Plain from southern Virginia to southern Alabama. . . . . 7b. 1. Drylands variant of *A. virginicus* var. *glaucus.*
            4. Pubescence below raceme sheath sparse to dense; raceme sheaths (2.4–)3.2–4.8(–6) cm long; racemes (1.5–)2–3(–4) cm long; spikelets (3–)3.5–3.9(–4.9) mm long; plants of poorly drained soils on Coastal Plain from southern New Jersey to eastern Texas. . . . . 7b. 2. Wetlands variant of *A. virginicus* var. *glaucus.*
    2. Leaves green (sometimes slightly glaucous in *A. gyrans* var. *stenophyllus* and smooth variant of *A. virginicus* var. *virginicus*).
        5. Stem sheaths scabrous with upwardly directed prickle hairs; leaf blades usually more than 35 cm long.
            6. Ligules usually less than 1 mm long; raceme sheaths usually less than 2.5 mm wide; keels of lower glume often scabrous below middle. . . . . 9d. 1. Robust variant of *A. glomeratus* var. *pumilus.*

6. Ligules usually more than 1 mm long; raceme sheaths mostly more than 2.5 mm wide; keels of lower glume glabrous or scabrous below middle only in southwestern variant of *A. glomeratus* var. *pumilus.*

7. Keels of lower glume rarely scabrous below middle; plants of eastern United States.

8. Inflorescences (linear to) oblong; spikelets usually less than 4 mm long; anthers usually marcescent within spikelets; peduncles less than 10 mm long; plants of Coastal Plain from southern Virginia to southern Mississippi. .... 9b. *A. glomeratus* var. *hirsutior.*

8. Inflorescences oblong to obpyramidal; spikelets usually more than 4 mm long; anthers usually not marcescent within spikelet; usually some mature peduncles more than 10 mm long; plants ranging from Massachusetts to southern Mississippi on Coastal Plain and well inland. .... 9a. *A. glomeratus* var. *glomeratus.*

7. Keels of lower glume usually scabrous below middle; plants of southwestern United States. .... 9d. 2. Southwestern variant of *A. glomeratus* var. *pumilus.*

5. Stem sheaths smooth, very rarely scabrous; leaf blades usually less than 35 cm long (except in robust variant of *A. glomeratus* var. *pumilus*).

9. Inflorescence units largely hidden within broadened, strongly overlapping uppermost stem sheaths. .... 2a. 1. Common variant of *A. gyrans* var. *gyrans.*

9. Inflorescence units mostly exposed at maturity.

10. Leaves glabrous.

11. Ligules (0.8–)1.1(–1.5) mm long, with ciliations less than 0.1 mm long; basal leaves often filiform, less than 1.5 mm wide, strongly erect. .... 2b. *A. gyrans* var. *stenophyllus.*

11. Ligules less than 0.7 mm long (rarely to 1 mm, but usually longer in southwestern variant of *A. glomeratus* var. *pumilus*), with ciliations usually greater than 0.1 mm long; basal leaves usually more than 2 mm wide, soon arching.

12. Stem internodes glaucous; some inflorescence units (especially at stem and branch apices) with 3 or more racemes.

13. Stems less than 1 m long; inflorescence units less than 14 per stem; spikelets usually more than 4 mm long. .. .. 2a. 2. Tenuous variant of *A. gyrans* var. *gyrans.*

13. Stems more than 1 m long; inflorescence units usually more than 14 per stem; spikelets usually less than 4 mm long. .... 7a. 3. Smooth variant of *A. virginicus* var. *virginicus.*

12. Stem internodes green, or glaucous just below node only; inflorescence units with 2 racemes (infrequently more).

14. Ligules more than 1 mm long; keels of lower glume often scabrous to below middle; spikelets usually greater than 4 mm long; plants of southwestern United States and northwestern Mexico. .... 9d. 2. Southwestern variant of *A. glomeratus* var. *pumilus.*

14. Ligules less than 1 mm long; keels of lower glume scabrous only above middle; spikelets less than 4 mm long; plants of southeastern United States. .... 7a. 2. Deceptive variant of *A. virginicus* var. *virginicus.*

10. Leaves pubescent, at least on margin near collar.

15. Keels of lower glume often scabrous below middle; leaves usually more than 44 cm long.

16\. Spikelets usually less than 4 mm long; ligules (0.6–)0.8(–1.3) mm long; raceme sheaths usually less than 2.5 mm wide; wide-ranging plants of most of temperate North and Central America except southwestern United States. .... 9d. 1. Robust variant of *A. glomeratus* var. *pumilus*.

16\. Spikelets usually longer than 4 mm; ligules (1–)1.5(–2.2) mm long; raceme sheaths usually more than 2.5 mm wide; plants of southwestern United States and northwestern Mexico. .. .. 9d. 2. Southwestern variant of *A. glomeratus* var. *pumilus*.

15\. Keels of lower glume scabrous only above middle; leaves usually less than 31 cm long.

17\. Pubescence of young stem sheaths appressed; spikelets usually more than 4 mm long; hairs on rachis internode and pedicel dense, long. .... 6. *A. longiberbis*.

17\. Pubescence of young stem sheaths spreading; spikelets mostly less than 4 mm long; hairs on rachis internode and pedicel rather sparse, short.

18\. Raceme sheaths (2.7–)3.3–4.4(–5.5) mm wide; racemes often more than 2 per inflorescence unit; widespread through most of eastern United States, absent from all but southernmost Florida. .... 7a. 1. Old-field variant of *A. virginicus* var. *virginicus*.

18\. Raceme sheaths (1.7–)2.4–3.1(–4) mm wide; racemes usually 2 per inflorescence unit; Coastal Plain from Florida to southern Virginia, common only in Florida. .... 7a. 2. Deceptive variant of *A. virginicus* var. *virginicus*.

1\. One or more postflowering peduncles more than 15 mm long.

19\. All raceme sheaths largely hidden before senescence within broadened, strongly overlapping, uppermost stem sheaths. .... 2a. 1. Common variant of *A. gyrans* var. *gyrans*.

19\. Most or all raceme sheaths clearly exposed after anthesis; uppermost stem sheaths reduced, not strongly overlapping.

20\. Inflorescence units with (2 to) 4 to 6 (to 13) racemes.

21\. Stems less than 0.9 m tall; leaves less than 15 cm long; stem sheaths more or less glabrous (to densely pubescent); spikelets less than 4.2 mm long; plants of Mexico. .... 4a. *A. liebmannii* var. *liebmannii*.

21\. Stems more than 0.8 m tall; leaves more than 15 cm long; stem sheaths usually densely woolly-pubescent, at least near collar; spikelets more than 4.2 mm long; plants of United States. .... 4b. *A. liebmannii* var. *pungensis*.

20\. Inflorescence units with 2 (or more) racemes.

22\. Stem sheaths scabrous with upwardly directed prickle hairs.

23\. Rachis internodes becoming sparsely pubescent toward base; stem sheaths usually more or less pubescent; plants of moist or disturbed ground.

24\. Ligules (1–)1.2(–2) mm long, with ciliations less than 0.3 mm long; keels of lower glume scabrous only above middle. .... 9a. *A. glomeratus* var. *glomeratus*.

24\. Ligules (0.6–)0.8(–1.3) mm long, with ciliations 0.2–0.9 mm long; keels of lower glume often scabrous below middle. .... 9d. 1. Robust variant of *A. glomeratus* var. *pumilus*.

23\. Rachis internodes densely and uniformly pubescent, not becoming sparsely pubescent toward base; stem sheaths rarely pubescent; plants of sandy uplands. .... 5. *A. floridanus.*

22. Stem sheaths smooth.

25. Many or all peduncles longer than raceme sheaths at maturity, racemes then fully exserted above apex of raceme sheath.

26. Racemes usually less than 2.1(–2.6) cm long; inflorescence branches long and arching, inflorescences open, loose. .... 8. *A. brachystachyus.*

26. Racemes exceeding 2 cm in length, usually more than 2.5 cm long; inflorescence branches erect, inflorescences more or less dense.

27. Stems less than 0.9 m tall; leaves less than 2 mm wide; some racemes usually fully included within raceme sheaths at maturity on peduncles less than 10 mm long; anthers often marcescent. .... 2a. 2. Tenuous variant of *A. gyrans* var. *gyrans.*

27. Stems usually more than 1 m tall; leaves mostly more than 3 mm wide; racemes rarely included within raceme sheaths at maturity, peduncles rarely less than 15 mm long; anthers rarely marcescent.

28. Leaves glabrous, blade mostly more than 35 cm long; stamen 1 per flower, anther less than 2 mm long. .... 5. *A. floridanus.*

28. Leaves often pubescent, blade less than 35 cm long; stamens 3 per flower (if only 1, anther more than 2 mm long).

29. Stamen(s) mostly 1; lower glumes more or less folded; awns less than 1 cm long. .... 1. *A. arctatus.*

29. Stamens 3; lower glumes flat; awns more than 1 cm long.

30. Lower glume nerved between keels (most easily seen on adaxial surface); endemic of Florida. .... *A. ternarius* var. *cabanisii.*

30. Lower glume not nerved between keels; widespread through most of eastern United States. .... *A. ternarius* var. *ternarius.*

25. Peduncles all shorter than raceme sheaths, at least bases of racemes not fully exserted above raceme sheath apices.

31. Stems less than 1.2 m tall; leaf blades less than 30 cm by 3 mm; inflorescence units rarely more than 20 per stem.

32. Raceme sheaths (2.2–)2.5–3.8(–4.5) cm long; spikelets usually less than 4 mm long. .... 7a. 2. Deceptive variant of *A. virginicus* var. *virginicus.*

32. Raceme sheaths usually more than 4 cm long; spikelets generally more than 4 mm long.

33. Ligules more than 0.8 mm long, with ciliations less than 0.1 mm long; plants of bogs and ditches. .... 2b. *A. gyrans* var. *stenophyllus.*

33. Ligules less than 0.8 mm long, with ciliations often more than 0.2 mm long; plants of well-drained soils.

34. Spikelets (4–)4.8–5(–5.5) by 0.6–0.8 mm; racemes paired; anthers more than 1.2 mm long. .... 3. *A. tracyi.*

34. Spikelets (3.5–)4–4.5(–5.2) by 0.5–0.6 mm; racemes 2 to 4 per inflorescence unit; anthers less than 1.2 mm long. .... 2a. 2. Tenuous variant of *A. gyrans* var. *gyrans*.

31. Stems usually more than 1.2 m tall; leaf blades often more than 30 cm by 3 mm; inflorescence units usually more than 20 per stem.

35. Racemes usually less than 2.1(–2.6) cm long; inflorescence branches long and arching, inflorescences open, loose. .. .. 8. *A. brachystachyus*.

35. Racemes often longer than 2 cm; inflorescence branches erect (infrequently somewhat spreading in deceptive variant of *A. virginicus* var. *virginicus*), inflorescences more or less dense.

36. Rachis internodes densely and uniformly pubescent, not becoming sparsely hairy toward base; many peduncles regularly more than 30 mm long. .... 5. *A. floridanus*.

36. Rachis internodes sparsely pubescent toward base; peduncles rarely more than 20 mm long.

37. Raceme sheaths (1.5–)2–2.5(–3) mm wide; keels of lower glume often scabrous below middle; stems to 2.5 m tall; leaves to 109 cm by 9.5 mm. .... 9d. 1. Robust variant of *A. glomeratus* var. *pumilus*.

37. Raceme sheaths (1.7–)2.4–3.1(–4) mm wide; keels of lower glume scabrous only above middle; stems less than 1.7 m tall; leaves less than 35 cm by 5.5 mm. .... 7a. 1. Deceptive variant of *A. virginicus* var. *virginicus*.

1. **Andropogon arctatus** Chapman, Bot. Gaz. **3:** 20. 1878. Based on *Andropogon tetrastachyus* Ell. var. *distachyus* Chapman, Fl. So. U. S. 581. 1860. Not *Andropogon distachyus* L., 1753. TYPE:[2] Florida, *Chapman s.n.* (lectotype, NY!). FIGURES 11, K; 34.

Sorghum arctatum (Chapman) Kuntze, Rev. Gen. Pl. **2:** 791. 1891.

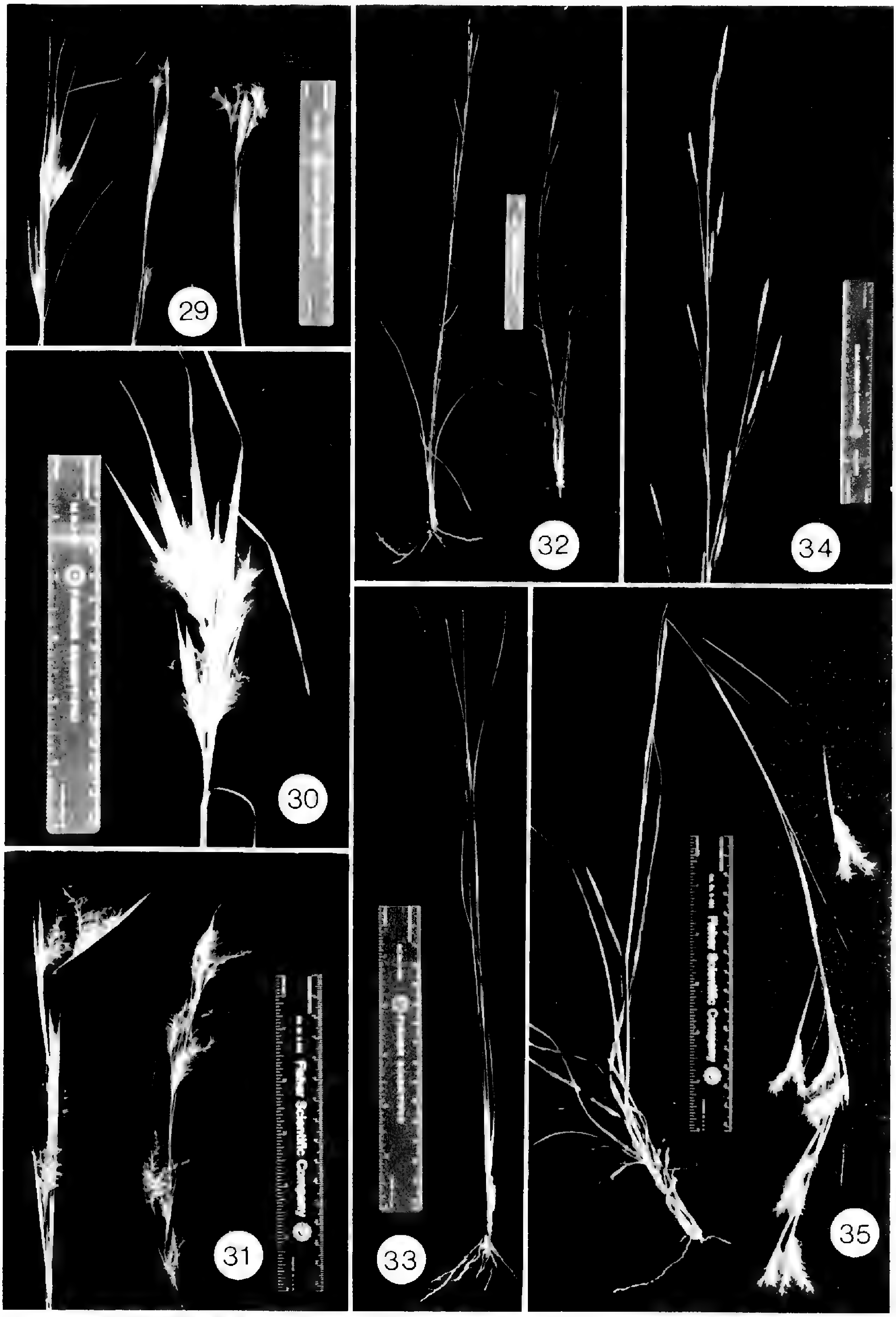
Leptopogon carinatus (Nees) G. Roberty subvar. *arctatus* (Chapman) G. Roberty, Boissiera **9:** 197. 1960.

DIAGNOSIS. Inflorescence units averaging 16 per stem; peduncles all long; spikelets long and wide, the lower glume more or less concave at maturity, with keels scabrous to below middle; anthers long, red; flowers rarely, if ever, chasmogamous.

DISTRIBUTION. Flatwoods, bogs, and scrublands. Florida (except extreme south and Suwannee River drainage) and southern Alabama (MAP 5).

REPRESENTATIVE SPECIMENS. **United States.** FLORIDA: Bay, *Godfrey 76774* (FSU); Brevard, *Fredholm 6110* (US); Calhoun, *Woods s.n.*, 1954 (TENN); Charlotte, *Lewis 107* (US); Clay, *Swallen 5584* (US); Collier, *Lakela 31145* (DUKE); Escambia, *Campbell 3944*; Franklin, *Hausman s.n.*, 1867 (NY); Gulf, *Silveus 6735-A* (TAES); Highlands, *Campbell 4118* (GH); Hillsborough, *Shuey 1507* (USF); Jackson, *Godfrey et al. 76736* (FSU); Liberty, *Godfrey*

[2] A Chapman specimen from NY, annotated in his script, is here designated the lectotype.



FIGURES 29–35. 29–31, *Andropogon gyrans* var. *gyrans*, inflorescences: 29, common variant (*Campbell 4143*), from one population, showing variation from mostly cleistogamous (left) to mostly chasmogamous (right) flowering; 30, common variant (*Campbell 4095*), senescent; 31, tenuous variant, showing plants with predominantlv cleistogamous (left, *Campbell 3746*) and mostly chasmogamous (*Campbell 3873*) flowers. 32, 33, *A.*

74577 (FSU, NCU, VDB); Manatee, *Simpson s.n.*, 1889 (GH); Osceola, *Ray et al. 10490* (GH, US, USF); Santa Rosa, *Combs 486* (US); Walton, *A. H. Curtiss 6924* (GH, MO, US); Washington, *Combs 661* (US). ALABAMA: Covington, *Kral 44769* (GH, VDB).

Andropogon arctatus is unique in the virginicus complex in four respects. First, it does not grow in the Suwannee straits, a corridor along the Suwannee River from the Okefenokee Swamp in southern Georgia to the Gulf of Mexico. The distribution of other members of the virginicus complex that are common in Florida includes the Suwannee straits.

Second, it appears to have a life history different from that of the successful colonizing taxa of the virginicus complex. The six densest populations of this taxon observed in my field studies grew in recently burned areas. Three of these were clear-cut slash pine (*Pinus elliottii* Engelmann) timberlands in northwestern Florida, where fire is routinely used by the forestry industry in site preparation. One of these localities, in Liberty County, was observed by Dr. Robert K. Godfrey in 1976; the following year there were only a few individuals where there had previously been hundreds. The same marked reduction in the number of flowering plants occurred in the other two "pine fields" in the second year after site preparation. In one of these localities, numerous basal clumps of leaves of this species were found in the third year. It appears that *Andropogon arctatus* remains in this vegetative state until it is burned, then flowers abundantly before returning to a vegetative state. Restriction of flowering to a year or two following fire probably accounts in large part for the supposed rarity of this taxon. (Removal of the forest canopy by heavy winds or lumbering operations may, in certain circumstances, also stimulate flowering.) Although other andropogons are stimulated by fire (FIGURE 26), the number of their flowering stems tends to increase greatly two and three years later. Also, the other andropogons infect a burned site with dispersal units from nearby populations rather than remaining in situ until fire occurs.

Third, in contrast to the mostly cespitose habit of the rest of the virginicus complex, the base of the plant of *Andropogon arctatus* is a short, rather thick rhizome.

Fourth, the anthers of *Andropogon arctatus* are longer than those of any other taxon in the virginicus complex: the lower limit of the range of *A. arctatus* overlaps the upper limit of that of only *A. brachystachyus*. Although the flowers of *A. arctatus* usually have one stamen, out of 138 flowers from six individual plants in one population in Liberty County, Florida (*Campbell 4060*), 68 percent had one stamen, 29 percent two, and 3 percent three. In the virginicus complex as a whole, the frequency of two- and three-stamened flowers is less than 0.1 percent. In addition to stamen number and anther length, other features associated with chasmogamy—long peduncles and large spikelets—point to the relatively primitive position of *A. arctatus* in the virginicus complex.

In overall aspect *Andropogon arctatus* closely resembles *A. ternarius*, which is the only other common United States species in sect. LEPTOPOGON outside the virginicus complex. *Andropogon ternarius*, however, is an unlikely ancestor

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gyrans var. *stenophyllus* (*Campbell 3813*): 32, two stems; 33, basal leaves. 34, *A. arctatus* (*Campbell 3944*), inflorescence. 35, *A. tracyi* (*Campbell 4100*), stem. Scale = 15 cm.

of *A. arctatus* because it is tetraploid. *Andropogon ternarius* var. *cabanisii* (Hackel) Fern. & Griscom (chromosome number unknown) differs from *A. arctatus* only in stamen number and in the size and intercarinal nerves of the lower glumes. Knowledge of the chromosome number of *A. ternarius* var. *cabanisii* is necessary to clarify its relationship to *A. arctatus.*

The closest relatives of *Andropogon arctatus* in the virginicus complex are probably *A. floridanus* and the common variant of *A. gyrans* var. *gyrans.* All three taxa may produce very long peduncled racemes that are more or less densely pubescent with whitish hairs.

2. **Andropogon gyrans** Ashe, Jour. Elisha Mitchell Sci. Soc. **15:** 113. 1898. NEOTYPE: North Carolina, Wake or Orange County, *Ashe 2034,* 1896 (NCU!).

DIAGNOSIS. Stems short; leaves narrow; inflorescences little branched and bearing few inflorescence units; raceme sheaths long and wide; peduncles all short or short and long on same plant; racemes long; callus hairs long (except taxon 2b).

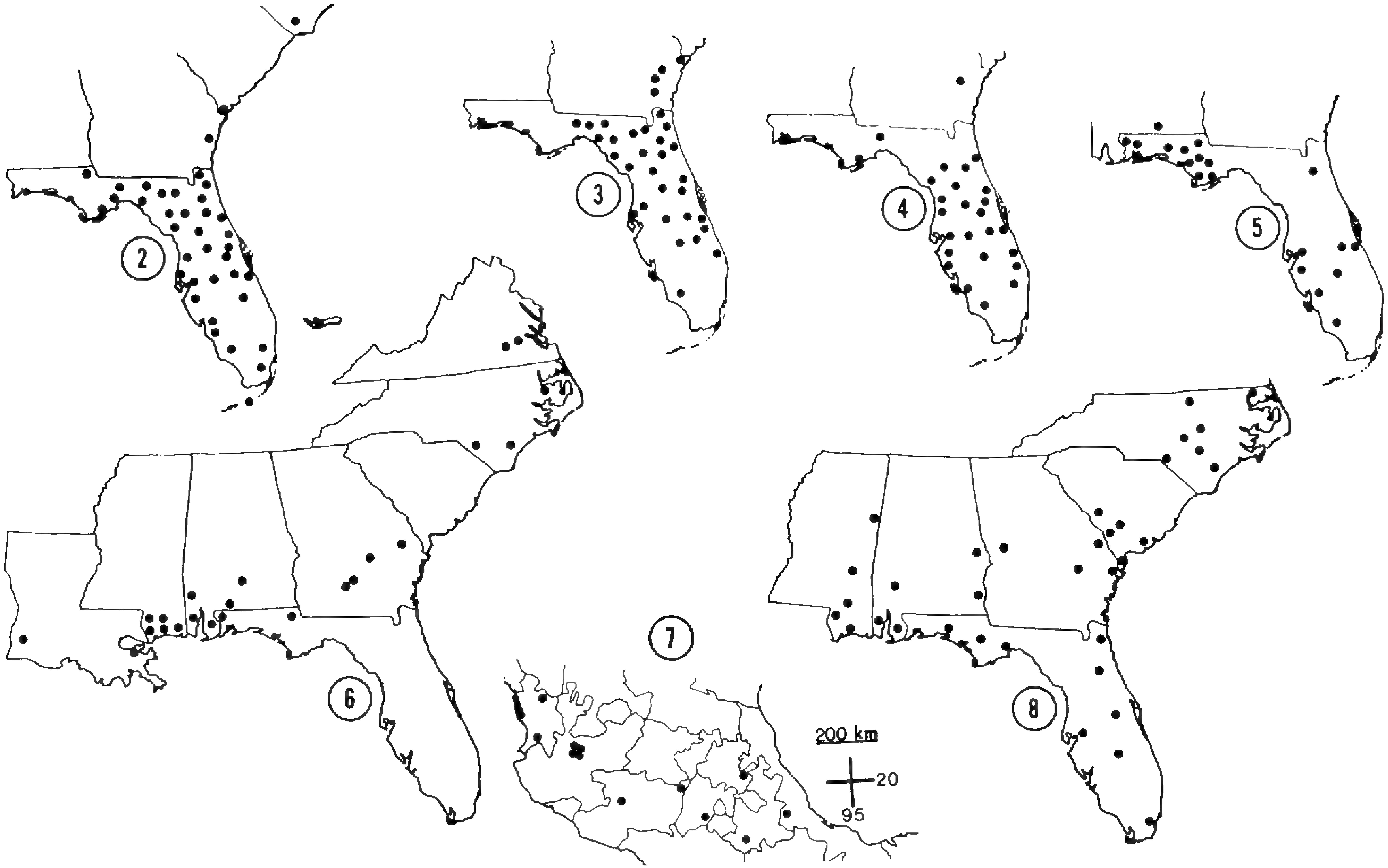
DISTRIBUTION. Dry or wet soils. New Jersey to Missouri, south to Florida and Texas; rare in Central America and West Indies.

This common and widespread taxon has long been known as *Andropogon elliottii* Chapman. Chapman published this name (Fl. So. U. S. 581. 1860) as new for *A. argenteus* Ell. (Bot. S. Carolina Georgia **1:** 148. 1816), a later homonym of *A. argenteus* DC. (1813). Elliott's description and type (Scribner, 1901), however, clearly place this name in synonymy with *A. ternarius* Michaux (1803). The synonymy of *A. ternarius* is presented in APPENDIX D.

The next oldest name at the species level is *Andropogon clandestinus* Wood, a later homonym of *A. clandestinus* Nees (see synonymy under taxon 2a below). The next available name is *A. gyrans.*

The specimen chosen as the neotype matches Ashe's protologue in most respects. The stems on this sheet fit his description in stem height, leaf-sheath glabrousness, and raceme number. The specimen label bears, in Ashe's script, the following information: "*Andropogon.* On sandstone between [?] and Chapel Hill, N.C. Wake or Orange Co. No. 2034 Date Oct 1896 Coll. W.W. Ashe." At the end of his protologue, Ashe stated "collected by the writer in pine woods in Durham county, N.C., Oct. 1896." It should be noted that Wake and Orange counties lie on either side of Durham County. It may well be that this specimen was the basis for Ashe's *Andropogon gyrans* and that the discrepancies of label and protologue are due to his carelessness. This specimen cannot, however, be definitely tied to Ashe's name and so is designated as neotype.

The equivalence of Ashe's specimen to the widespread taxon long known as *Andropogon elliottii* is questionable. The upper stem sheaths of this species are usually conspicuously overlapping and inflated, a distinctive and unique feature; those of the neotype are remote and not inflated. Less striking characters (short stems, dense hairs at the base of the raceme sheaths, number of racemes per inflorescence unit, long callus hairs, and twisting of the bases of the awns), however, clearly equate the neotype with the widespread taxon. This specimen



Maps 2–8. Distributions: 2, *Andropogon longiberbis*; 3, *A. brachystachyus*; 4, *A. floridanus*; 5, *A. arctatus*; 6, *A. liebmannii* var. *pungensis*; 7, *A. liebmannii* var. *liebmannii* (central Mexico); 8, *A. tracyi*.

and a few others from throughout the Coastal Plain of the southeastern United States are intermediate between the common and tenuous variants of *A. gyrans* var. *gyrans*; they appear to be plants of the common variant in which overlapping and inflation of the upper stem sheaths are not strongly expressed.

There are two clusters of characters uniting the three taxa of this species. First, they are all small plants with small inflorescences, but the inflorescence unit and many of its parts are larger than those of most other taxa. This contrast of sizes provides a quick means of distinguishing these three taxa from depauperate individuals of *Andropogon virginicus*. Second, the other broomsedges have either all short peduncles, all long peduncles, or more or less continuous variation from short to long within a single plant. Variation is bimodal on an individual in the common variant of *A. gyrans* var. *gyrans*, or between individuals in the tenuous variant and *A. gyrans* var. *stenophyllus*, since some have only short peduncles and some mostly long peduncles. Occasionally, short- and long-peduncled plants of these two taxa occur in the same population, but more often they are separated in different populations. This bimodality reflects a variability that tends to correspond to ecological and geographic differences.

Hackel's subvar. *stenophyllus* is here made a variety of *Andropogon gyrans* for the first time. In addition to the characters uniting this taxon to the common and tenuous variants of var. *gyrans* discussed above, var. *stenophyllus* is separated from these two variants by a distance of 5 (TABLE 6).

Key to the Subspecific Taxa of *Andropogon gyrans*

1. Ligules usually less than 0.8 mm long; plants of well-drained soils, rarely of poorly drained sites.
    2. Raceme sheaths usually hidden within inflated, strongly overlapping upper stem sheaths. .... 2a. 1. Common variant of *A. gyrans* var. *gyrans*.
    2. Raceme sheaths mostly visible. .... 2a. 2. Tenuous variant of *A. gyrans* var. *gyrans*.
1. Ligules (0.8–)1.1(–1.5) mm long; plants of bogs and ditches. .... 2b. *A. gyrans* var. *stenophyllus*.

2a. **Andropogon gyrans** Ashe var. **gyrans**

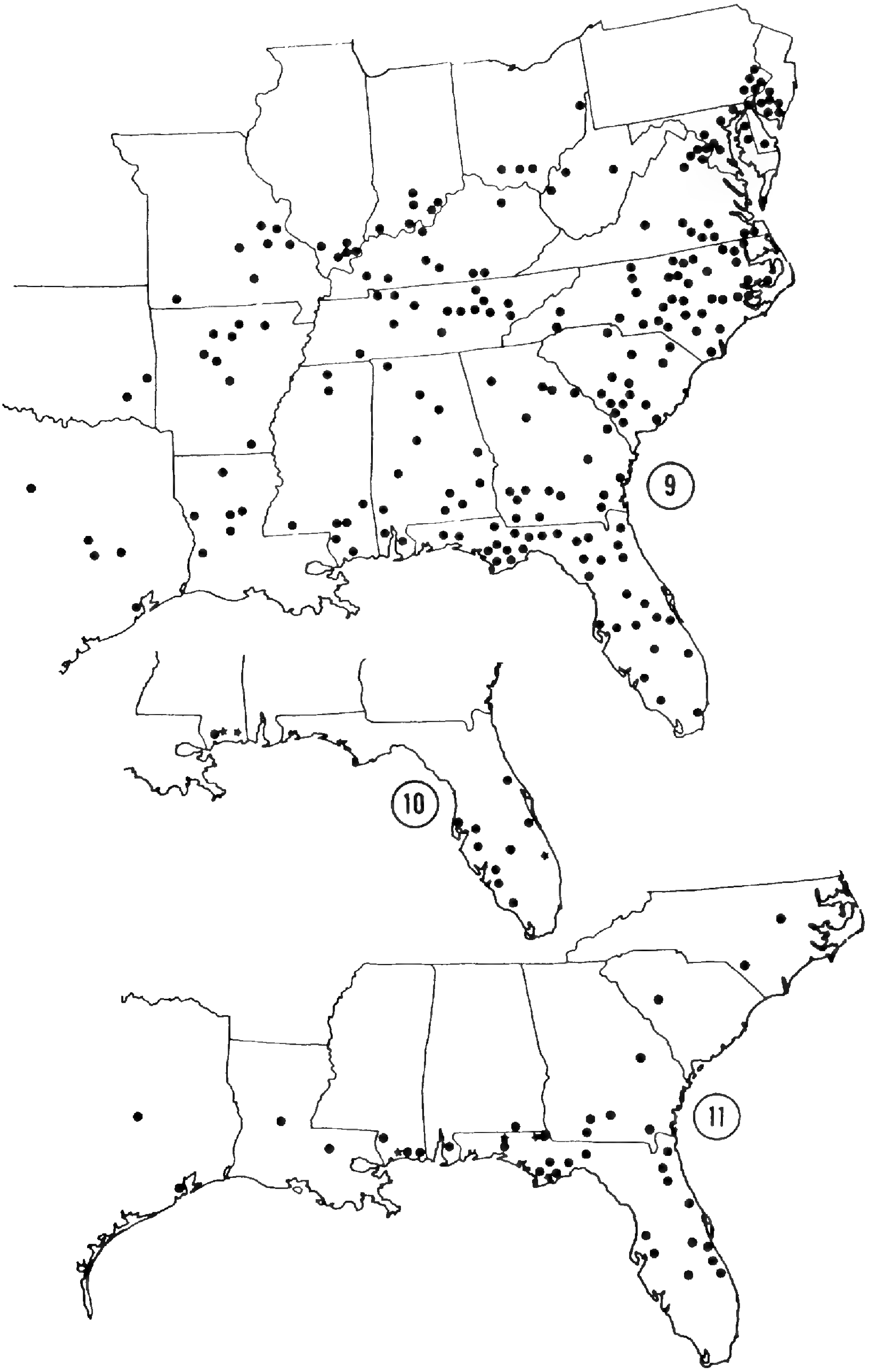
Andropogon clandestinus Wood, Class-book Bot. 809. 1861, *ex char.* (as *clandestina*). Not *Andropogon clandestinus* Nees, 1854. TYPE: unknown.

Andropogon elliotti Chapman var. *gracilior* Hackel in DC. Monogr. Phanerog. **6**: 415. 1889. TYPE: Florida, Duval County, *A. H. Curtiss 3636a* (holotype, not seen; isotypes, DUKE!, FSU!, GA!, GH!, MICH!, MISSA!, MO (two sheets)!, NCU!, US!). *Andropogon gracilior* (Hackel) Nash in Small, Fl. SE. U. S. 63. 1903. *Andropogon elliottii* Chapman f. *gracilior* (Hackel) Blomq. Grasses N. Carolina, 203. 1948.

Andropogon campyloracheus Nash, Bull. New York Bot. Gard. **1**: 431. 1900. Based on *Andropogon elliottii* Chapman var. *laxiflorus* Scribner, Bull. Torrey Bot. Club **23**: 146. 1896. Not *Andropogon laxiflorus* Steudel, 1854. TYPE: Florida, Lake County, *Nash 1738*, 1894 (holotype, US!; isotypes, GH!, MICH!). *Anatherum virginicum* (L.) subvar. *laxiflorum* (Scribner) G. Roberty, Boissiera **9**: 213. 1960.

Andropogon subtenuis Nash in Small, Fl. SE. U. S. 63, 64. 1903. TYPE: Mississippi, Harrison County, *Tracy 2243*, 1896 (holotype, NY!).

Andropogon virginicus L. var. *graciliformis* León, Bull. Torrey Bot. Club **53**: 457. 1926.



Maps 9–11. Distribution of *Andropogon gyrans*: 9, var. *gyrans*, common variant (also outside United States; see representative specimens); 10, var. *gyrans*, tenuous variant; 11, var. *stenophyllus*. (In 10 and 11 dots represent populations of plants with short peduncles; stars, populations of plants with long peduncles.)

Type: Cuba, Santa Clara, Sabana de Montembo, *León & Loustalot 11343* (holotype, Colegio de la Salle, Vedado, Havana, not seen; isotype, GH!).

Andropogon elliottii Chapman var. *projectus* Fern. & Griscom, Rhodora **37**: 138, 139. 1935. Type: North Carolina, Buncombe County, *Baltimore 1421*^{c}, 1898 (holotype, GH!; isotypes, NCU!, NY!, US (two sheets)!).

Diagnosis. Ligules short.

Distribution. Same as the species.

2a. 1. **Common variant** Figures 11, A, B; 29; 30.

Diagnosis. Raceme sheaths hidden within overlapping and more or less inflated upper stem sheaths.

Distribution. Generally dry, sandy soil of roadsides, embankments, fields, pine or oak woods; occasionally in moister soil. New Jersey to Missouri, south to Florida and Texas; Mexico (Beetle, 1977); Belize; Honduras; Cuba (Map 9).

Representative specimens. **United States.** New Jersey: Atlantic, *Long 14026* (GH); Camden, *Long 15430* (GH); Cape May, *Mackenzie 6695* (DUKE, MICH, MO, NY); Cumberland, *Long 29696* (GH); Gloucester, *Lippincott s.n.*, 1894 (GH); Salem, *Long s.n.*, 1909 (GH, NY). Pennsylvania: Bucks, *Long 65639* (GH); Chester, *Pennell 8889* (NY); Delaware, *Bartram 1383* (GH); Montgomery, *Fogg 5384* (GH); Philadelphia, *Crosby s.n.*, 1942 (GH). Delaware: New Castle, *Long 57766* (GH); Sussex, *Churchill s.n., s.d.* (MO). Maryland: Baltimore, *Taylor s.n.*, 1890 (MICH); Caroline, *Wilkens 5057-a* (NCU); Cecil, *Tatnall 4411* (GH); Montgomery, *Hitchcock 251* (GH, MO, NY, US); Prince George's, *Blake 9733* (GH); Queen Anne's, *Commons s.n.*, 1870 (NY). District of Columbia: *Steele s.n.*, 1896 (DUKE, GH, NY). West Virginia: Cabell, *Millender s.n.*, 1939 (NY); Jackson, *Richardson s.n.*, 1955 (NCU). Virginia: Arlington, *Allard 91a* (DUKE, GH, MO, NY); Bedford, *A. H. Curtiss 9868* (MO); Brunswick, *Fernald & Lewis 14475* (GH); Culpepper, *Ahles & James 61644* (NCU); Dinwiddie, *Swallen 5527* (US); Fairfax, *Fosberg 30198* (GH); Fauquier, *Allard 3891* (GH); Greensville, *Fernald & Long 9250* (GH); Lunenburg, *Ahles & James 61944* (NCU); Nansemond, *Fernald & Long 6761* (GH, MO, NY); Norfolk, *Kearney 2383* (US); Northampton, *Fernald et al. 5786* (GH); Prince Edward, *Ahles & James 62685* (NCU); Prince William, *Hermann 9911* (GH, MO, NY). North Carolina: Anson, *Correll 7091* (DUKE, GA, MICH); Beaufort, *Ashe* (NCU); Bertie, *Ahles & Haesloop 52163* (NCU); Buncombe, *Biltmore 1421*^{b} (GH, NCU, NY, US); Granville, *Dayton 1715* (NCU); Harnett, *Boyce et al. 1608* (NY, US); Gates, *Godfrey 7039* (DUKE, GH); Forsyth, *Ahles & Haesloop 51646* (NCU); Durham, *Godfrey 6729* (GH); Davidson, *Denke s.n.*, 1826 (DUKE); Cumberland, *Ahles 36592* (FSU, NCU); Craven, *Blomquist 11423* (DUKE); Brunswick, *Blomquist 413* (GH); Bladen, *Ahles 37423* (NCU, USF); Hertford, *Ahles & Haesloop 52209* (NCU); Hyde, *Radford 42668* (NCU); Lee, *Correll 6977* (DUKE, GH); Lenoir, *Radford 31634* (NCU); Mecklenberg, *Batson 408* (DUKE); Moore, *Correll 7214* (DUKE); Nash, *Godfrey & Kerr 6644* (DUKE, GH); Northampton, *Ahles 52459* (NCU); Orange, *Blomquist 466* (DUKE); Pamlico, *Radford 42295* (NCU); Pender, *Ashe 319* (NCU); Person, *Bowmer 147* (NCU); Richmond, *Correll 7134* (DUKE, GH); Sampson, *Campbell 3994* (GH); Scotland, *Godfrey 6946* (GH); Stokes, *Ashe s.n.*, 1896 (NCU); Transylvania, *Cain 265* (TENN); Wake, *Blomquist 119* (US); Wayne, *Radford 31497* (NCU); Vance, *Ahles & Leisner 20288* (NCU). South Carolina: Aiken, *Ahles & Crutchfield 55181* (NCU); Allendale, *Bell 5124* (NCU, US); Bamberg, *Campbell 4008* (GH); Barnwell, *Batson & Kelley s.n.*, 1959 (NCU); Calhoun, *Ahles 35306* (GA, NCU); Charleston, *Ahles & Haesloop 38652* (NCU); Dillon, *Ahles 37103* (GH, NCU); Dorchester, *Ahles & Haesloop 37859* (NCU); Florence, *Campbell 3967* (GH); Hampton, *Ahles & Bell 20922* (NCU); Kershaw, *Radford 30043* (NCU, NY); Lexington, *Radford 29877* (NCU, VDB); Orangeburg, *Ahles 35136* (NCU); York, *Ahles 34490* (NCU).

GEORGIA: Baker, *Godfrey 67566* (FSU, US); Bartow, *Duncan et al. 12110* (GA); Berrien, *Celarier A-2588-1* (MO); Brantley, *Campbell 4026* (GH); Butts, *Campbell 4143* (GH); Calhoun, *Thorne 6863* (GA); Charlton, *Campbell 4139* (GH); Clarke, *Miller s.n.*, 1941 (US); Decatur, *Godfrey 74097* (FSU, NCU); Dougherty, *Eyles 7666* (DUKE); Lincoln, *Pyson & McVaugh 92* (GA); McIntosh, *Bozeman & Ahles 2476* (NCU); Oglethorpe, *Harper 656* (DUKE, GA); Screven, *Eyles 7569* (DUKE); Tift, *Celarier A-2608-1* (MO); Toombs, *Duncan & Hardin 14522* (NCU); Thomas, *Campbell 4180* (GH). FLORIDA: Alachua, *Swallen 5626* (US); Bay, *Godfrey 61605* (FSU); Brevard, *Fredholm 6134* (GH, US); Calhoun, *Godfrey 61601* (DUKE, FSU, US, USF, VDB); Clay, *Campbell & Godfrey 4139* (GH); Collier, *Deam 65368* (US); Columbia, *DeSelm s.n.*, 1969 (TENN); Dade, *Eaton s.n.*, 1903 (GH, US, VT); Duval, *A. H. Curtiss 3636a* (FSU, GH, MICH, MISSA, MO, NCU, US); Franklin, *Campbell 3932* (GH); Gadsden, *Godfrey 64939* (FSU, VDB); Gilchrist, *Godfrey 65098* (FSU); Gulf, *Silveus 6732-A* (GA, TAES); Highlands, *Brass 15647* (GH, US); Hillsborough, *Lakela 23700* (FSU, US, USF); Jackson, *Campbell 3782* (GH); Jefferson, *Campbell 4069* (GH); Lake, *Silveus 6689* (TAES); Lee, *Kellogg 27041* (MO); Leon, *Kral 1805* (DUKE, FSU, NY); Levy, *Campbell 4095* (GH); Liberty, *Godfrey 73140* (FSU); Madison, *Kral 6188* (DUKE, FSU, GH, VDB); Martin, *Campbell 3872* (GH); Okaloosa, *Godfrey 76203* (FSU); Pinellas, *Tracy 7768* (GH, MO, NY, WIS); Polk, *Lakela 23588* (USF, VDB); Putnam, *Godfrey & Morrill 52629a* (DUKE, FSU); Orange, *Baker 63* (US); Osceola, *Fredholm 6098* (GH); Suwannee, *DeSelm s.n.*, 1969 (TENN); Wakulla, *Godfrey & Morar 61587* (DUKE, FSU, US); Walton, *Godfrey 55250a* (FSU, GH, NCU, USF). OHIO: Highland, *Braun s.n.*, 1961 (US); Jackson, *Bartley & Pontius 814* (NY, US); Jefferson, *Jones s.n.*, 1935 (NY); Pike, *Bartley 2989* (NY); Vinton, *Musgrove 770* (NCU). INDIANA: Clark, *Seaver 26865* (GH, US); Floyd, *Deam 51650* (US); Lawrence, *Kriebel 1441* (DUKE); Orange, *Deam 33395½* (US); Perry, *Deam 39976* (US); Vanderburgh, *Deam 33104* (US). KENTUCKY: Barren, *Braun 3636* (US); Christian, *Labisky 279* (WIS); Edmonson, *Braun 3563* (US); Fleming, *Braun 1743* (GH, US); Lyon, *Athey 3877* (FSU); McCreary, *Braun 482* (US); Meade, *Sargent 100* (GH); Wayne, *Braun 2834* (US). TENNESSEE: Blount, *Thomas s.n.*, 1964 (TENN); Coffee, *Gattinger s.n.*, 1880 (MICH); Cumberland, *Jennison 3394* (TENN); Davidson, *Gattinger s.n., s.d.* (NY); Fentress, *Rogers 41376* (TENN); Hickman, *Kral 4357* (VDB); Knox, *Ruth s.n.*, 1894 (NY); McNairy, *Shanks et al. 14704* (TENN); Montgomery, *Shanks 1077* (TENN); Morgan, *Rogers 41376* (NCU); Roane, *Rogers 41402* (NCU, TENN, VDB); Stewart, *Ellis & Clebsch 930* (NCU); Van Buren, *Iltis 3405* (TENN); White, *DeSelm 218* (TENN). ALABAMA: Baldwin, *Kral 29768* (VDB); Barbour, *Kral 38017* (VDB); Bibb, *Campbell 3959* (GH); Coffee, *Kral 41685* (VDB); Covington, *Kral 33656* (TENN, VDB); Cullman, *Eggert s.n.*, 1898 (MO); Crenshaw, *Kral 41605* (VDB); Lauderdale, *Kral 29353* (GA, VDB); Lee, *Earle & Baker s.n.*, 1897 (MICH, MO, NCU, NY); Marengo, *Kral 29588B* (FSU, VDB); Mobile, *Mohr s.n.*, 1889 (NY); St. Clair, *Kral 37930* (VDB); Washington, *McDaniel 9915* (GA, VDB). MISSISSIPPI: Amite, *Ray 5471* (MISSA); Forest, *Rogers 7045* (NCU, TENN); Harrison, *Tracy 8394* (GH, MO, NY, US, WIS); Lafayette, *Burke 66* (MISS); Lamar, *Jones 2951* (GA); Marshall, *Lasseter 589* (MISS); Pearl River, *Reed 34* (FSU, VDB); Wayne, *Kearney 163* (US). ILLINOIS: Hardin, *Evers 21903* (MO, WIS); Saline, *Evers 67370* (NCU, WIS). MISSOURI: Barry, *Mackenzie s.n.*, 1896 (NY); Franklin, *Shea 299* (MO); Jefferson, *Eggert s.n.*, 1886 (GH); Phelps, *Steyermark 20905* (MO); Shannon, *Steyermark 16339* (GH, MO); St. Genevieve, *Steyermark 8290* (GH, MO); Washington, *Steyermark 77858* (US). ARKANSAS: Ashley, *Iltis 25312* (WIS); Conway, *Moore 321046* (WIS); Izard, *Robinson 2134A* (GH, NY, US); Lawrence, *Robinson 2223* (NY); Pope, *Lawson s.n.*, 1949 (NCU); Pulaski, *Engelmann 78* (MO); Searcy, *Robinson 2184* (US); Stone, *Hatcher s.n.*, 1951 (NCU). LOUISIANA: Beauregard, *Heyne 1381* (US); Grant, *Ewen 17506* (MO); LaSalle, *Swallen 10501* (US); Lincoln, *Kral 16119* (FSU, VDB); Rapides, *Cassady s.n.*, 1952 (TAES); Sabine, *Kral 16219* (FSU, VDB). OKLAHOMA: Le Flore, *Waterfall 9848* (US). TEXAS: BRAZOS, *Sperry 2566* (TAES); Erath, *Hancock 64-8* (TAES); Galveston, *Waller & Bauml 3208A* (GH, TAES); Robertson, *Lincecum 31* (TAES); Walker, *McCleod s.n.*, 1957 (TAES). **Belize.** El Cayo Distr., San Augustin, *Lundell 6727* (MICH, NY). **Honduras.** El Paraíso, *Standley 29035* (F). **Cuba.** LAS VILLAS: Santa Clara, Sabana de Motembo, *León 11343* (GH).

I include three previously described varieties in the common variant, so called because of its high frequency of occurrence in nature. Scribner distinguished his *Andropogon elliottii* var. *laxiflorus* from *A. elliottii* Chapman var. *elliottii* on the basis of the upper stem sheaths of the former not being inflated and overlapping. In addition, he noted the long rachis internodes ("joints") of his variety. In Florida, Mississippi, Louisiana, and South Carolina there are at least eight populations that resemble Scribner's type in having all the internodes of the upper part of the stem elongate. While these elongations make the plants quite distinctive, they appear to represent merely an abnormality of plants of the common variant of *A. gyrans* var. *gyrans*. One of the specimens (*Nash 1759* (NY!)) cited by Nash in his protologue of *A. campyloracheus* (based on *A. elliottii* var. *laxiflorus*) as being from the type locality has two stems that are connected at the base. One of these has the elongate internodes of Scribner's *A. elliottii* var. *laxiflorus,* and the other has the overlapping, inflated upper stem sheaths characteristic of the common variant of *A. gyrans* var. *gyrans*. The cause of this possible abnormality is unknown, but two observations may be of importance. First, all these abnormal plants flower earlier than is normal for the common variant. Second, half of the populations contain some plants that are viviparous, the flowers being replaced by small plantlets. It is not known whether or not these plantlets are effective in reproducing the parent plant. Their frequency of occurrence in nature in the virginicus complex as a whole is extremely low.

Fernald and Griscom named *Andropogon elliottii* var. *projectus* without appreciating the variability of peduncle length, the single distinguishing character of this variety. There is more or less continuous variation between plants with short peduncles and entirely hidden (and cleistogamous-flowered) racemes, and plants with some racemes hidden and some exposed on long peduncles. Very infrequently, some plants may have all or many of the racemes exserted above the apex of the raceme sheaths. Moreover, the claim that this taxon has a "notable geographic segregation" (Fernald & Griscom, 1935) is unsupportable since there does not appear to be any geographic pattern to variation in peduncle length.

Andropogon elliottii var. *gracilior* was based solely on overall plant size. I have seen populations of noticeably smaller individuals. They do not seem to be juvenile since their size remained consistent over the two years during which I observed them. Their size is apparently not a phenotypic response to poor soil conditions since I have seen short and tall plants within 50 m of one another in a uniform flatwoods locality in southern Florida. Regardless of these observations, plant size is far too variable in the common variant to warrant recognition of this variety.

2a. 2. **Tenuous variant** FIGURES 11, E, F; 31.

DIAGNOSIS. Raceme sheaths visible after anthesis.

DISTRIBUTION. Sandy, moist or dry soil. Florida and Mississippi (MAP 10).

REPRESENTATIVE SPECIMENS. **United States.** FLORIDA: Brevard, *Campbell 3765* (GH); Charlotte, *Hitchcock 440* (GH); Collier, *Lakela 31196* (GH); Franklin, *Godfrey 75579* (FSU);

Highlands, *Campbell 3746* (GH); Hillsborough, *Lakela 25249* (GH); Lee, *Hitchcock 440* (GH, MO, NY, US); Manatee, *Perdue 1789* (FSU, GH, NCU, TAES, USF); Martin, *Campbell 3873* (GH); Pinellas, *Lakela 27621* (USF); Volusia, *Shuey & Poppleton 1544* (USF). MISSISSIPPI: Harrison, *Tracy 4701* (GH, TAES, US); Jackson, *Tracy 2243* (NY).

This taxon includes two kinds of plants. One has both long- and short-peduncled racemes—and hence both chasmogamous and cleistogamous flowers—on the same stem. I have seen this kind only once (Florida, Martin Co., *Campbell 3873*) in the field. There are two other populations in southern Mississippi (MAP 10), one of which is the source of the lectotype of *Andropogon subtenuis* Nash (*Tracy 2243* (NY); Hitchcock, 1951). The second kind has only short peduncles and predominantly cleistogamous flowers. It has neither been described formally nor discussed in any previous publications concerning the virginicus complex. Invariably it has been identified as *A. virginicus.*

As its name implies, the tenuous variant is difficult to circumscribe. It differs from the common variant quite strikingly in the one character provided in their diagnoses. Nevertheless, there are plants of intermediate morphology that are not readily placed into either taxon. The best way to distinguish the tenuous variant from *Andropogon gyrans* var. *stenophyllus* is by comparing the ligules; the latter taxon also occurs more frequently and ranges farther in more poorly drained soils.

2b. **Andropogon gyrans** Ashe var. **stenophyllus** (Hackel) Campbell, comb. nov. FIGURES 11, C, D; 32; 33.

BASIONYM: *Andropogon virginicus* L. subvar. *stenophyllus* Hackel in DC. Monogr. Phanerog. **6:** 411. 1889. TYPE:[3] Florida, *Chapman s.n., s.d.* (lectotype, W!; isolectotype, W!). *Andropogon virginicus* L. var. *stenophyllus* (Hackel) Fern. & Griscom, Rhodora **37:** 142. 1935.

Andropogon perangustatus Nash in Small, Fl. SE. U. S. 62. 1903. Based on *Andropogon virginicus* L. subvar. *stenophyllus* Hackel. Not *Andropogon stenophyllus* Roemer & Schultes, 1817.

DIAGNOSIS. Ligules long, with marginal ciliations short.

DISTRIBUTION. Ditches, bogs, savannas, and pond margins. Coastal Plain from North Carolina to eastern Texas (MAP 11).

REPRESENTATIVE SPECIMENS. **United States.** NORTH CAROLINA: Robeson, *Ahles 37246* (NCU); Wilson, *Radford 40687* (NCU). SOUTH CAROLINA: Saluda, *Radford 30369* (NCU). GEORGIA: Berrien, *Harper 1707* (GH, MO); Charlton, *Campbell 4138* (GH); Colquitt, *Godfrey 76086* (FLAS); Emanuel, *Plummer & Pullen 1962* (GA); Thomas, *Campbell 41481* (GH). FLORIDA: Brevard, *Fredholm 6193* (US); Clay, *Campbell 4137* (GH); Duval, *A. H. Curtiss 6016* (FSU, GA, GH, MO, NCU, NY, TAES, US, VT); Franklin, *Campbell 3822* (GH); Gulf, *Chapman s.n.* (GH, MO); Highlands, *Swallen 5368*; Hillsborough, *Fredholm 6427* (GH); Indian River, *Tracy 9298* (TAES, US); Jackson, *Campbell 3813* (GH); Jefferson, *Campbell 4070* (GH); Liberty, *Campbell 3829* (GH); Osceola, *Fredholm 6072* (US); Pasco, *Ray 9594* (US, USF); Putnam, *Godfrey 76892* (FSU); St. Lucie, *Silveus 6664* (TAES); Volusia, *Silveus 6529* (DUKE, GA, TAES); Wakulla, *Lamp 17* (FSU); Walton, *A. H. Curtiss 6928*

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[3] Hackel cited "Florida (Chapman) et Alabama (Mohr)." There are two Chapman sheets of a Florida collection and one Mohr collection (Alabama, Mobile County, *s.n.*) in the Hackel herbarium at W. One of the Chapman specimens is here designated the lectotype.

(GA, GH, MO, NY, US). ALABAMA: Baldwin, *Kral 38228* (GH, US, VDB); Geneva, *Kral 52006* (VDB). MISSISSIPPI: Harrison, *Tracy 3830* (MICH, MO, NY); Jackson, *Earle 1890* (TAES); Pearl River, *Reed 40* (FSU). LOUISIANA: East Baton Rouge, *Brown 1499* (US); Grant, *McKellar 272* (US); Rapides, *Duncan 1956* (TAES). TEXAS: Galveston, *Waller & Bauml 3325* (GH, TAES); Robertson, *Hatch 2108* (TAES).

Like the tenuous variant of *Andropogon gyrans* var. *gyrans, A. gyrans* var. *stenophyllus* consists of two kinds of plants differing in flowering mode. The short-peduncled, cleistogamously flowering plants tend to grow in relatively disturbed sites such as roadside ditches and have a much wider range than the mostly long-peduncled and often chasmogamous plants. I have seen only three populations of the latter kind, all in infrequently disturbed boggy sites. Two of the populations contained predominantly chasmogamous-flowered plants. In the third locality, a rather wet flatwoods in Franklin County, Florida, was a mixture of the two flowering modes (*Campbell 3822*), with the chasmogamous type predominating. The two types of plants differ in three ways (see TABLE 7), which hold for nonmixed populations of both kinds of plants. It is not known whether or not these two kinds are genetic segregates of one another. They are not separated as taxa because they do not differ morphologically in any ways other than the three usually correlated characters, and these characters vary within a single population.

3. **Andropogon tracyi** Nash, Bull. New York Bot. Gard. **1**: 433. 1900. TYPE: Mississippi, Lowndes County, *Tracy 3083,* 1895 (holotype, NY!).
FIGURES 11, T; 35.

DIAGNOSIS. Stems short; leaves narrow; inflorescence units few per stem; peduncles, spikelets, and anthers long.

DISTRIBUTION. Sandhills, sandy pinelands and scrublands. Coastal Plain from North Carolina to Mississippi (MAP 8).

REPRESENTATIVE SPECIMENS. **United States.** NORTH CAROLINA: Gates, *Ahles & Duke 51584* (NCU); Granville, *Dayton 1267* (NCU); Harnett, *Radford 8762* (NCU); Johnston, *Radford 29156* (NCU); Pender, *Wells s.n.,* 1925 (NY); Sampson, *Campbell 3993* (GH); Scotland, *Ahles 36966* (NCU). SOUTH CAROLINA: Aiken, *Miller s.n.,* 1966 (NCU); Allendale, *Campbell 3716* (GH); Bamberg, *Campbell 4007* (GH); Beaufort, *Cuthbert s.n.,* 1902 (FLAS); Charleston, *Ahles & Haesloop 38051* (NCU). GEORGIA: Chatham, *Eyles 6645* (US); Screven, *Campbell 4203* (GA); Talbot, *Jones s.n.,* 1959 (GA); Toombs, *Hardin & Duncan 14526* (GA). FLORIDA: Bay, *Kral 52173* (VDB); Dade, *Small et al. 897* (NY); Calhoun, *Grelen 11/58-7* (FSU); Duval, *A. H. Curtiss 4012a* (NY); Highlands, *Davis s.n.,* 1941 (FLAS); Hillsborough, *Fredholm 6423* (US); Orange, *Baker 329* (S); Putnam, *Campbell 4100* (GH); Walton, *McDaniel 7145* (FSU, VDB). ALABAMA: Baldwin, *Kral 29797* (US, VDB); Clarke, *Kral 29570B* (VDB); Henry, *Kral 48974* (VDB); Lee, *Earle & Baker 1456* (MO, NY, US); Mobile, *Langlois s.n.,* 1880 (MO); Pike, *Kral 52222* (VDB). MISSISSIPPI: Forrest, *Rogers 7047* (NCU, VDB); Harrison, *Earle s.n.,* 1899 (NY); Jasper, *McDaniel 2796* (MO, NY); Lowndes, *Tracy s.n.,* 1895 (US); Pearl River, *Sargent 8668* (VDB).

Earlier workers have noted a similarity between *Andropogon tracyi* and *A. longiberbis,* and the two species are indeed similar in general aspect. They differ, however, in overall size, in amount and orientation of leaf pubescence, and in length of the peduncle, spikelet, and anther. *Andropogon tracyi* also has

Table 7. **Comparison of the morphology of two kinds of plants* of Andropogon gyrans var. stenophyllus.**

Mean (± S.E.) percent chasmogamy	Sample size	Peduncle length (mm)	Spikelet length (mm)	Anther length (mm)
73 (8)†	9	(8–)12–22(–45)	(4.4–)4.7–5.2(–5.5)	(1.1–)1.4–1.5(–1.7)
30 (6)	4	(4.5–)5–5.5(–6)	(4–)4.2–4.5(–5.2)	(0.9–)1–1.2(–1.3)

*Both kinds from *Campbell 3822,* Franklin County, Florida.

†For the meaning of the measurements in this table, see explanation in Character States section.

a wider, more northerly range. It is possible that a shift in flowering mode toward cleistogamy in the ancestral stock of *A. tracyi* may have given rise to ancestors of *A. longiberbis.* However, in the other instances in the complex where such a change in flowering mode can be inferred, there is a pronounced similarity in other specialized characters that strongly tie the taxa to one another. No such specialized characters in *A. tracyi* and *A. longiberbis* suggest a common ancestry.

The resemblance of *Andropogon tracyi* and *A. gyrans,* particularly the tenuous variant of var. *gyrans,* is also great. The tenuous variant has peduncles that are either variable or all short on an individual plant, smaller spikelets, and shorter anthers.

4. **Andropogon liebmannii** Hackel, Flora **68:** 132. 1885. Type:[4] Mexico, Chinantla, *Liebmann 77* (lectotype, c!; isolectotypes, c!, gh (two sheets)!, mich!, uc (two sheets)!, us (three sheets)!). *Sorghum liebmannii* (Hackel) Kuntze, Rev. Gen. Pl. **2:** 792. 1891. *Anatherum virginicum* (L.) Sprengel subvar. *liebmannii* (Hackel) G. Roberty, Boissiera **9:** 213. 1960.

Diagnosis. Peduncles all long, usually bearing 4 or more racemes; raceme sheaths long; spikelets broad.

Distribution. Generally moist ground. Mexico and Coastal Plain of southeastern United States.

The two varieties of *Andropogon liebmannii* have been treated as distinct species by most American authors. However, the morphological distance of 9 separating them (Table 6) is based primarily on differences of size, which possibly arise either from dissimilar growing conditions in Mexico and the

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[4] Although Hackel cited *Liebmann 590* from Chinantla, Mexico, A. F. Maule of the Botanical Museum in Copenhagen notes (pers. comm.) that Liebmann's numbers were not collector's numbers but a systematic arrangement after his return; no. *590* was at Berlin and destroyed(?). Several other Liebmann specimens from Chinantla (none of them from w) bear Hackel's determination. One of these has been chosen as the lectotype. Hackel also cited *Bourgeau 2376,* but the only specimen of this collection that I have examined (Mexico, Veracruz, 1865–1866 (gh!)) bears no indication that Hackel saw it.

southeastern United States or from pleiotropy of one or more genes controlling size. The two varieties share a character state (raceme number—character 22 of TABLE 4) found only in these two taxa, and they are strongly similar in most qualitative characters, flowering mode, and preference for wet soils.

4a. **Andropogon liebmannii** Hackel var. **liebmannii** FIGURE 36.

Andropogon liebmannii Hackel subvar. *raripilus* Hackel in DC. Monogr. Phanerog. **6:** 413. 1889. TYPE: Mexico, Jalisco, *Palmer 227,* 1886 (holotype, not seen; isotypes, GH!, UC!, VT!).

DIAGNOSIS. Small (in stem height, leaf-blade length, maximum inflorescence branching and sympodia, and inflorescence units per stem); leaves often only sparsely pubescent.

DISTRIBUTION. Swales, banks, fields, and pinelands to 2200 m alt. Central volcanic belt of Mexico (MAP 7).

REPRESENTATIVE SPECIMENS. **Mexico.** NAYARIT: Tepic, *Rose 2222* (GH), *McVaugh et al. 16434* (MICH). JALISCO: Los Colomos, *Villarreal de Puga 4061* (MICH); near Guadalajara, *Palmer 227* (GH, UC, VT), *Pringle 11212* (F, GH, VT). MICHOACÁN: near Ciudad Hidalgo, *Gould 9613* (UC), *Kral 25539* (VDB); Uruapan, *Hitchcock 263* (F, GH, UC). MÉXICO: Temascaltepec, *Hinton 1413* (GH). PUEBLA: Chinantla, *Liebmann s.n.,* 1841 (C, GH, MICH, UC). HIDALGO: Agua Blanca, *Moore 2064* (GH). VERACRUZ: Tzuatlanchillo, *Bourgeau 2376* (GH).

Andropogon liebmannii var. *liebmannii* flowers during August and September, and infrequently in May and June. It is either a rather rare or an undercollected taxon presently known from only 12 localities.

4b. **Andropogon liebmannii** var. **pungensis** (Ashe) Campbell, comb. nov. FIGURES 11, J; 37; 38.

BASIONYM: *Andropogon mohrii* (Hackel) Vasey var. *pungensis* Ashe, Jour. Elisha Mitchell Sci. Soc. **15:** 113. 1899. TYPE: North Carolina, Washington County, *Ashe 1898* (holotype, NCU!).

Andropogon liebmannii Hackel subvar. *mohrii* Hackel in DC. Monogr. Phanerog. **6:** 413. 1889. TYPE: Alabama, Mobile County, *Mohr s.n.,* 1888 (holotype, US!). *Andropogon mohrii* (Hackel) Vasey, Contr. U. S. Natl. Herb. **3:** 11. 1892. *Anatherum virginicum* (L.) subvar. *mohrii* (Hackel) G. Roberty, Boissiera **9:** 213. 1960.

DIAGNOSIS. Large (relative to var. *liebmannii* in characters listed in diagnosis of that taxon); leaves usually densely pubescent.

DISTRIBUTION. Bogs, swamps, savannas, and flatwoods. Coastal Plain from Virginia to Louisiana; relatively infrequent in Florida (MAP 6).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA: Dinwiddie, *Swallen 5541* (US); Prince George, *Fernald et al. 6758* (GH). NORTH CAROLINA: Pender, *Blomquist 10064* (DUKE, GH, NY, US); Robeson, *Ahles 37317* (NCU); Washington, *Ashe s.n.,* 1898 (NCU). GEORGIA: Bullock, *Plummer & Pullen s.n.,* 1962 (GA); Irwin, *Harper 1708* (GH, MO, NY); Tift, *Plummer & Pullen s.n.,* 1962 (GA); Wheeler, *Plummer & Pullen s.n.,* 1962 (GA). FLORIDA: Escambia, *Campbell 3948* (GH); Franklin, *Godfrey 79254* (FSU); Jackson, *Campbell 3913* (GH); Liberty, *Godfrey 78259* (FSU); Washington, *Godfrey 80130* (FSU).

FIGURES 36–41. 36, *Andropogon liebmannii* var. *liebmannii* (*Kral 25539*, Mexico), portion of inflorescence. 37, 38, *A. liebmannii* var. *pungensis* (*Campbell 3948*): 37, portion of inflorescence; 38, stem. 39, 40, *A. floridanus* (*Campbell 4194*): 39, basal clump of leaves; 40, inflorescences at different stages (left, mature fruit; middle, young fruit; right, anthesis). 41, *A. longiberbis* (*Campbell 4098*), two inflorescences. Scale = 15 cm.

ALABAMA: Baldwin, *Tracy 8604* (GH, MO, TAES, US); Butler, *Kral 41632* (VDB); Escambia, *Kral 44845* (VDB); Mobile, *Mohr s.n., s.d.* (MISSA, NCU, NY, TAES, US); Washington, *Kral 29542* (NCU, VDB). MISSISSIPPI: Hancock, *Rogers 2498* (NCU, TENN, VDB); Harrison, *Tracy 3895* (DUKE, GH, NCU, NY, US, W); Jackson, *Demaree 34499* (GA, MISSA, TAES, US, VDB); Pearl River, *Sargent 9027* (GA, MISS); Stone, *DeSelm 1969* (TENN). LOUISIANA: Orleans, *Drummond s.n.*, 1832 (NY); Calcasieu, *Drummond s.n.*, 1833 (US).

Andropogon liebmannii var. *pungensis* forms small, infrequent populations in little-disturbed boggy sites. The often densely pubescent stem sheaths, the number of racemes per inflorescence unit, and the large spikelets make this variety easily identifiable. Some botanists have confused it with the old-field variant of *A. virginicus* var. *virginicus* (e.g., Kral's (1976) report of this taxon from Franklin County, Florida, is based on *Kral 52387,* which is actually the old-field variant of *A. virginicus* var. *virginicus*). These two taxa are similar in their densely pubescent stem sheaths and numerous racemes per inflorescence unit. They are best distinguished by peduncle length and spikelet dimensions.

5. **Andropogon floridanus** Scribner, Bull. Torrey Bot. Club **23:** 145. 1896. TYPE: Florida, Lake County, *Nash 1572,* 1894 (holotype, US!; isotypes, GH!, US (two sheets)!). *Anatherum virginicum* (L.) Sprengel subvar. *floridanum* (Scribner) G. Roberty, Boissiera **9:** 212. 1960.
FIGURES 11, H; 39; 40.

Andropogon bakeri Scribner & Ball, Bull. U. S. D. A. Div. Agrost. **24:** 39. 1901. TYPE: Florida, Orange County, *Baker 58,* 1897 (holotype, US, not seen; isotypes, GH!).

DIAGNOSIS. Leaves long, glabrous; peduncles long; hairs of rachis internode uniformly distributed, not becoming sparse toward base.

DISTRIBUTION. Sandy soils in southeastern Georgia and Florida; in *Pinus clausa* (Chapman) Vasey scrublands in eastern Florida (MAP 4).

REPRESENTATIVE SPECIMENS. **United States.** GEORGIA: Long, *Bozeman 1979* (GA, NCU). FLORIDA: Alachua, *Gould 6671* (TAES); Brevard, *Fredholm 6008* (GH, MO, US); Citrus, *Combs 976* (GH, US); Collier, *Lakela 31191* (GH, USF); Franklin, *Silveus 6503* (TAES, US); Hernando, *Ray 9530* (GH, NCU, US, VDB); Highlands, *Campbell 3887* (GH); Hillsborough, *Garber 1877* (GH, VT, W); Lake, *Nash 1681* (GH, NY, US); Lee, *Chase 4176* (US); Leon, *Kral 1801* (DUKE); Levy, *Cooley et al. 7174* (NCU, USF, WIS); Manatee, *Combs 1291* (US); Marion, *Campbell 4194* (GH); Martin, *Campbell 3754* (GH); Orange, *Campbell 3860* (GH); Osceola, *Fredholm 6072* (GH); Palm Beach, *Hitchcock 2264* (US); Polk, *Lakela 24273* (GH, NCU, USF); Putnam, *Laessle s.n.*, 1960 (US); St. John, *Silveus 6744* (US); St. Lucie, *Silveus 5294* (TAES); Sarasota, *Kral 51971* (VDB); Seminole, *Beardslee 41* (US); Volusia, *Hood 32* (US).

Plants of this species are easily distinguished from the rest of the virginicus complex by morphology and ecological preferences. The uniform distribution of pubescence on the rachis internodes is a unique and constant character. Laessle (1958) found *Andropogon floridanus* to be a good indicator of *Pinus clausa* scrub vegetation, an association confined to Florida. Other broomsedges may sometimes grow with *P. clausa,* but they characteristically invade more disturbed sites. *Andropogon floridanus* usually occurs in small populations of scattered individuals, but several stands of hundreds of individuals have been observed in clear-cut scrub pine (*P. clausa*) timberlands in central Florida.

6. **Andropogon longiberbis** Hackel, Flora **68:** 131, 132. 1885. TYPE:[5] Florida, *Garber 1877* (lectotype, W!; isolectotypes, MO!, NY!, US!, W (two sheets)!). *Sorghum longiberbe* (Hackel) Kuntze, Rev. Gen. Pl. **2:** 792. 1891. *Anatherum virginicum* (L.) subvar. *longiberbe* (Hackel) G. Roberty, Boissiera **9:** 213. 1960. FIGURES 11, I, J; 41.

DIAGNOSIS. Leaf pubescence mostly appressed; raceme sheaths rather broad; spikelets long; callus hairs long.

DISTRIBUTION. Sandy or rocky soils of roadsides, dunes, sandhills, pinelands, and fields. Southern South Carolina to Florida and Bahamas (MAP 2); common only in Florida.

REPRESENTATIVE SPECIMENS. **United States.** NORTH CAROLINA: New Hanover, *Schallert 1935* (DUKE). SOUTH CAROLINA: Beaufort, *Bell 1956* (NCU). GEORGIA: McIntosh, *Duncan 20605* (DUKE, FLAS, MISS, TENN, WIS). FLORIDA: Alachua, *Campbell 3854* (GH); Brevard, *Campbell 3764* (GH), *Small et al. 3352* (NY); Charlotte, *Parrott 81* (DUKE); Clay, *Campbell 4134* (GH); Collier, *Deam 60590* (DUKE); Columbia, *Godfrey 76903* (FSU); Dade, *Campbell 3729* (GH); Duval, *A. H. Curtiss 5571* (GA, GH, MO, NCU, NY); Flagler, *Young s.n.*, 1940 (GA); Franklin, *Godfrey 77349* (FSU); Gilchrist, *Campbell 3910* (GH); Hernando, *Correll 5845* (GH, US); Hillsborough, *Lakela 24138* (FSU, GH, NCU); Jackson, *Campbell 4032* (GH); Lake, *Nash 645* (GH, NY, TAES, US); Lee, *Standley 169* (GH, NY, US); Leon, *Kral 1837* (GH); Levy, *Campbell 4097* (GH); Madison, *Godfrey 75784* (FSU); Manatee, *Rugel 232* (NY, US, USF); Marion, *Campbell 4108* (GH); Monroe, *Campbell 4225* (GH); Nassau, *Godfrey 74687* (FLAS); Okeechobee, *Silveus 5776* (US); Orange, *Baker 49* (GH, NY); Osceola, *DeSelm 1969* (TENN); Pinellas, *Tracy 7185* (GH, NY, TAES, US, W, WIS); Polk, *Cooley et al. 8251* (GH, USF); Putnam, *Campbell 4089* (GH); Seminole, *Schallert 20854* (WIS); Suwannee, *Campbell 3847* (GH); Taylor, *Godfrey 75778* (FSU); Volusia, *Hood 41* (US); Wakulla, *Campbell 4063* (GH). **Bahama Islands:** Grand Bahama, *Correll & Kral 43036* (VDB).

Andropogon longiberbis is related to several other members of the virginicus complex. It apparently hybridizes with both the old-field variant of *A. virginicus* var. *virginicus* and the robust variant of *A. glomeratus* var. *pumilus* (see section on hybridization), suggesting some affinities. The morphological gap of 6.5 between *A. longiberbis* and *A. virginicus* is the smallest of all interspecific gaps. Furthermore, the gaps between *A. longiberbis* and two of the three variants of var. *virginicus* are only 7 and 6.5. However, there are three morphological differences that always hold: leaf-pubescence orientation, callus-hair length, and spikelet length. These differences and the abundance of *A. longiberbis* in southernmost Florida (where *A. virginicus* is quite sparsely distributed) justify maintaining *A. longiberbis* as a distinct species.

Andropogon longiberbis and the robust variant of *A. glomeratus* var. *pumilus* differ in many ways, the most reliable being peduncle length, raceme-sheath width, spikelet dimensions, callus-hair length, and scabrousness of the lower glume keels.

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[5] Hackel cited "Florida leg. Garber, Curtiss." He apparently had at least three sheets of the first collection and one of the second (Florida, Duval County, *A. H. Curtiss 3638*, W!, FLAS!, US!) in his herbarium (the sheets are stamped "Herbarium E. Hackel"). One of the Garber sheets is here selected as the lectotype.

The possibility that *Andropogon longiberbis* is a cleistogamous derivative of ancestral stock of *A. tracyi* is discussed under that species.

About 10 percent of all the specimens of *Andropogon longiberbis* examined in this study bear vernal-flowering stems. Over 90 percent of the 29 plants flowering between February and July had charred basal leaves, indicating a recent fire and the possibility that burning stimulates flowering.

7. **Andropogon virginicus** L. Sp. Pl. 1046. 1753, not Sp. Pl. ed. 2. 1482. 1763 (= *Andropogon leucostachyus* HBK.). TYPE: America (holotype, LINN 1211.12, photo GH!). *Holcus virginicus* (L.) Steudel, Nom. Bot. ed. 2. **1:** 773. 1840, pro syn. *Sorghum virginicum* (L.) Kuntze, Rev. Gen. Pl. **2:** 792. 1891.

DIAGNOSIS. Ligules short, usually brownish and prominently ciliate margined; peduncles and spikelets short; anthers often marcescent within spikelet.

DISTRIBUTION. In more or less full sun and in all but poorest soils; extremely weedy. Massachusetts to Ontario and Michigan, south to Florida and Texas; Mexico and Central America; West Indies; Colombia; apparently naturalized in California, Hawaii, Japan, and Australia.

Andropogon virginicus is the most ubiquitous, weedy, and taxonomically complex broomsedge in the eastern United States. The old-field variant is an extraordinarily successful colonizer of moist, cleared ground at low elevations. The great variability of *A. virginicus* ties it to four of the other species of the complex: one or more of its variants resemble eight of the lowest-ranking taxa of these four species. The ancestral stock of *A. virginicus* is hypothesized to be *A. brachystachyus,* and its closest relative from a morphological standpoint is *A. longiberbis.* Finally, certain of its variants have been confused or lumped with three taxa of *A. glomeratus* and two of *A. gyrans.* These ties are considered in more detail in the discussion of these four species.

At the subspecific level there are two varieties of *Andropogon virginicus* that differ in leaf color (green vs. glaucous). At a still lower level the three variants of var. *virginicus* and the two of var. *glaucus* are so closely related to one another and are separated by such variable characters that to bring them into the formal nomenclatural scheme of the group is impractical.

The subspecific variation in this species reflects rapid and probably recent evolution. With the acquisition of the capability for cleistogamous flowering and the tremendous disturbance of the native vegetation by man has come an explosion of broomsedge populations. A possible phylogeny of this species and its closest relative, *Andropogon brachystachyus,* is discussed under the latter species.

Within *Andropogon virginicus* all of the distances between the five variants lie between 3 and 8.5 (TABLE 6). Due to the smallness of the morphological gaps between the variants of *A. virginicus,* they have all been combined into one species.

Key to the Subspecific Taxa of *Andropogon virginicus*

1. Leaves green. . . . . *A. virginicus* var. *virginicus.*
    2. Stem internodes green; leaves usually pubescent, at least on margin near collar.
        3. Raceme sheaths (1.7–)2.4–3.1(–4) mm wide; racemes (1.3–)1.5–2.3(–3) cm long; usually at least some peduncles more than 12 mm long. . . . . 7a. 1. Deceptive variant.
        3. Raceme sheaths usually more than 3.1 mm wide; some racemes longer than 3 cm; peduncles less than 12 mm long. . . . . 7a. 2. Old-field variant.
    2. Stem internodes glaucous; leaves glabrous. . . . . 7a. 3. Smooth variant.
1. Leaves glaucous. . . . . 7b. *A. virginicus* var. *glaucus.*
    4. Pubescence below raceme sheath absent; raceme sheaths (2.1–)2.6–3.8(–4.9) cm long; spikelets (2.6–)3.2–3.5(–3.9) mm long; racemes (1.4–)1.7–2.4(–3.2) cm long. . . . . 7b. 1. Drylands variant.
    4. Pubescence below raceme sheath sparse to dense; raceme sheaths (2.4–)3.2–4.8(–6) cm long; spikelets (3–)3.5–3.9(–4.4) mm long; racemes (1.5–)2–3(–4) cm long. . . . . 7b. 2. Wetlands variant.

7a. **Andropogon virginicus** L. var. **virginicus**

Cinna lateralis Walter, Fl. Carolin. 59. 1788. Type: presumably South Carolina (holotype, BM; photo, GH!).

Andropogon dissitiflorus Michaux, Fl. Bor. Am. **1:** 57. 1803 (as *dissitiflorum, nomen superfl.* for *Cinna lateralis* Walter and with the same type).

Andropogon vaginatus Ell. Bot. S. Carolina Georgia **1:** 148. 1816. Type: no indication of origin (holotype, CHARL[6]). *Andropogon virginicus* L. var. *vaginatus* (Ell.) Wood, Class-book Bot. 808. 1861. *Dimeiostemon vaginatus* (Ell.) Jackson, Index Kew. **1:** 760. 1893, *pro syn.*

Andropogon tetrastachyus Ell. Bot. S. Carolina Georgia **1:** 150. 1816. Type: South Carolina, Charleston (holotype, CHARL; photo, GH!). *Andropogon virginicus* L. var. *tetrastachyus* (Ell.) Hackel in DC. Monogr. Phanerog. **6:** 411. 1889. *Dimeiostemon tetrastachyum* (Ell.) Jackson, Index Kew. **1:** 760. 1893, *pro syn.* (as *tetrastachys*). *Anatherum virginicum* (L.) Sprengel subvar. *tetrastachyum* (Ell.) Roberty, Boissiera **9:** 213. 1960.

Andropogon eriophorus Scheele, Flora **27:** 51. 1844, *ex char.* Not *Andropogon eriophorus* Willd., 1805. Type: West Virginia, Charles Town (holotype, not seen).

Andropogon curtisianus Steudel, Syn. Pl. Glum. **1:** 390. 1854. Type: *M. A. Curtis s.n.* (CAEN, P,[7] not seen).

Andropogon virginicus L. subvar. *genuinus* Hackel in DC. Monogr. Phanerog. **6:** 410. 1889. *Andropogon virginicus* L. var. *genuinus* Fern. & Griscom, Rhodora **37:** 142. 1935. Both of the above names are based on *Andropogon virginicus* L.

Diagnosis. Leaves green (sometimes slightly glaucous in smooth variant); racemes often more than 2 per inflorescence unit.

Distribution. Same as species.

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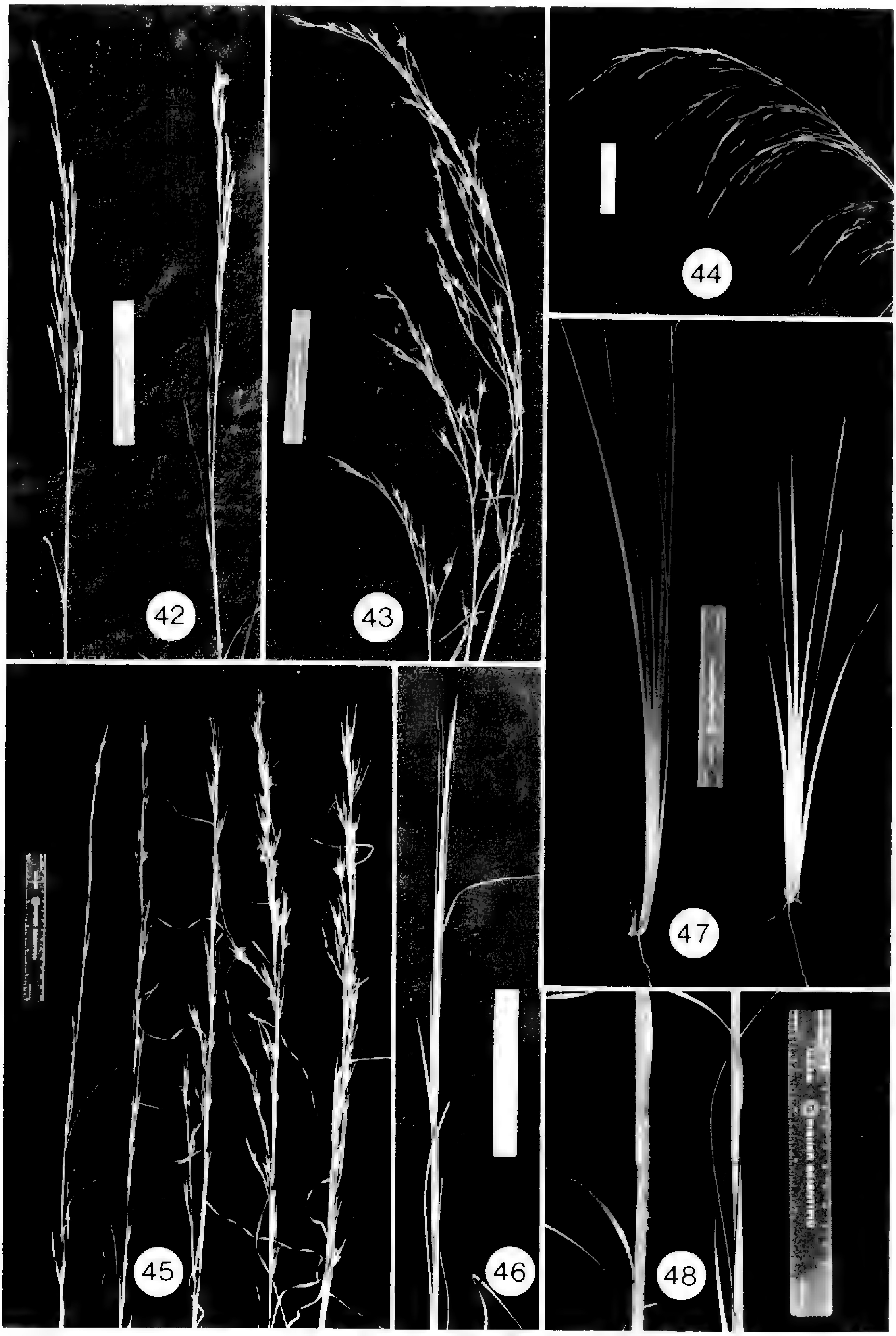
[6] Scribner (1901) and Weatherby (1942) placed this specimen in the taxon here recognized as *Andropogon virginicus* L. var. *virginicus.*

[7] Chase (1937) placed both of these sheets in the taxon here recognized as *Andropogon virginicus* L. var. *virginicus.*



FIGURES 42–48. 42–46, inflorescences: 42, deceptive variant of *Andropogon virginicus* var. *virginicus* (left, *Campbell 3747*) and drylands variant of *A. virginicus* var. *glaucus* (*Campbell 3898*); 43, drylands variant of *A. virginicus* var. *glaucus* (*Campbell 3865*); 44, *A. brachystachyus* (*Campbell 3884*); 45, old-field variant of *A. virginicus* var. *virginicus* (*Campbell 4144*); 46, smooth variant of *A. virginicus* var. *virginicus* (*Campbell 3902*).

7a. 1. Old-field variant

Figures 11, L, M; 45.

Diagnosis. Raceme sheaths wide; racemes usually 2 or more per inflorescence unit.

Distribution. Rapidly colonizing openings in mature vegetation created by disturbance; wide variety of soils, with some capacity for ecotypic differentiation (Chapman & Jones, 1975); to about 1000 m alt. in mountains. Massachusetts to Ontario, Michigan, and Iowa, south to northern Florida and Texas; distributed sporadically south of United States; naturalized in California, Hawaii, Japan, Australia, and perhaps elsewhere (Map 12).

Representative specimens. **Canada.** Ontario: Kent, *Catling et al. s.n.,* 1977 (MICH). **United States.** Massachusetts: Barnstable, *Fernald 435* (DUKE, GH, MICH, MISSA, MO, NCU (2 sheets), NY, WIS); Dukes, *Kennedy s.n.,* 1896 (GH (2 sheets)); Hampshire, *Ahles 84864* (CAS); Middlesex, *French s.n.,* 1888 (MO); Nantucket, *Bicknell s.n.,* 1904 (NY). Rhode Island: Washington, *Celarier A-2620-1* (MO); Newport, *Fernald et al. 8480, 8487* (GH). Connecticut: Fairfield, *Eames 8723* (USF); Hartford, *Bissell s.n.,* 1901 (GH, NY); Middlesex, *Gould 8832* (TAES); New Haven, *Allen s.n.,* 1877 (GH). New York: Bronx, *Bicknell 9656* (NY); New York, *Burnham 597* (GH); Suffolk, *Latham 29538* (GA). New Jersey: Atlantic, *Wagner 500* (MICH); Burlington, *Koster 05-53-2* (MICH); Cape May, *Mackenzie 6331* (DUKE, MO, NY); Middlesex, *Churchill s.n.,* 1889 (GH, MO); Ocean, *Mackenzie 2369* (MO, NY); Union, *Griscom 1500* (USF). Pennsylvania: Adams, *Loughridge 2767* (TAES); Berks, *Stoudt & Hermann 2728* (MICH); Dauphin, *Berkheimer 15262* (GH); Huntington, *Westerfield 19186* (NCU); Indiana, *Feduska s.n.,* 1958 (VT); Montgomery, *Dreisbach 1150* (MICH); Philadelphia, *Brenner 8351* (GH); York, *Pohl 1463* (WIS). Delaware: Kent, *Larsen 309* (GH); New Castle, *Canby s.n.,* 1899 (GH); Sussex, *Larsen 465* (DUKE, GH, MO). Maryland: Allegany, *Brown s.n.,* 1971 (NCU); Anne Arundel, *Smith s.n.,* 1879 (US); Harford, *Smith s.n.,* 1879 (US); Kent, *Campbell 4219* (GH); Queen Annes, *Campbell 4218* (GH); Talbot, *Earle 3734* (DUKE, GH). District of Columbia: *Chase 273* (GH, MO, NY, US (2 sheets)). West Virginia: Barbour, *Moore 2546* (GH, MICH); Cabell, *Gilbert 807* (GH, NY, TENN, WIS); Greenbrier, *Hunnewell 7222* (GH); Hampshire, *Downs 8980* (NCU); Kanawha, *Dennison s.n.,* 1966 (TAES); Monongalia, *Millspaugh 834* (NY); Randolph, *Greenman 79* (GH). Virginia: Arlington, *Allard 76* (MO); Bedford, *A. H. Curtiss s.n.,* 1872 (GH); Fauquier, *Allard 1134* (GH, NY); Frederick, *Hunnewell 11361* (GH); James City, *Menzel 334* (GH); Lunenburg, *Ahles & James 61945* (NCU); Northampton, *Fernald et al. 5187* (GH); Patrick, *Kral 9719* (NCU); Roanoke, *Wood 5742* (GH); Stafford, *Iltis 1047* (FSU). North Carolina: Alamance, *Ramseur & Hammond 2957* (DUKE, NCU); Anson, *Correll 7105* (DUKE, GH); Bertie, *Godfrey 7004* (DUKE, GH); Buncombe, *Biltmore 21*^{d} (GH, MO, NY); Caldwell, *Radford 19712* (DUKE, NCU); Craven, *Godfrey & White 6782* (DUKE, GH); Durham, *Blomquist 10180* (DUKE, NY); Gates, *Godfrey 7044* (DUKE, GH); Haywood, *Ahles & Duke 50305* (MISS, NCU); Hoke, *Ahles 36355* (NCU, WIS); New Hanover, *Schallert s.n.,* 1935 (DUKE, NCU); Rowan, *Small & Heller 349* (MO, NY). South Carolina: Aiken, *Ahles & Crutchfield 55214* (NCU); Allendale, *Bell 5204* (DUKE, NCU); Beaufort, *Bell 5249* (DUKE, NCU); Florence, *Campbell 4003* (GH); Jasper, *Bell 5293* (DUKE, NCU); Kershaw, *Radford 29927* (GH, NCU); Lee, *Radford 29382* (NCU, NY); Lexington, *Radford 29798* (GH, NCU). Georgia: Baker, *Thorne 6975* (GA); Bartow,

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47, *A. brachystachyus* (left, *Campbell 3884*) and drylands variant *A. virginicus* var. *glaucus* (*Campbell 3898*), basal clumps of leaves. 48, old-field (left) and smooth variants of *A. virginicus* var. *virginicus* (*Campbell 4133a, b,* St. Johns Co., Florida), stems. Scale = 15 cm.

Map 12. Distribution of old-field variant of *Andropogon virginicus* var. *virginicus*.

Greear 63371 (GA); Bullock, *Hall 221* (NCU); Butts, *Campbell 4144* (GH); Carroll, *Campbell 4147* (GH); Clarke, *Cronquist 4208* (GA, GH, NY); Coweta, *Campbell 4145* (GH); Dade, *Cronquist 4832* (GA, GH, NY); Evans, *Hardin & Duncan 14660* (GA, MICH); McIntosh, *Duncan 20605* (DUKE, GH, US, USF, WIS); Putnam, *Cronquist 4858* (GA, GH, MICH, MO, NY); Thomas, *Campbell et al. 4057* (GH); Walker, *Cronquist 4802* (GA, GH, MICH, NY); Wayne, *Campbell 4019* (GH). FLORIDA: Alachua, *Swallen 5558* (US); Baker, *Campbell 3849* (GH); Bay, *Godfrey 61631* (DUKE, FSU, USF); Calhoun, *Godfrey 61600* (FSU, USF); Collier, *Cooley et al. 9010* (FSU, GH, TENN, USF); Dade, *Atwater GS 156* (FSU, USF); Dixie, *Godfrey 56153* (FSU, NY); Duval, *A. H. Curtiss 3636* (DUKE, GA, MISSA, MO, NCU, NY); Escambia, *Campbell 3949* (GH); Franklin, *Kral 52387* (US); Gilchrist, *Godfrey 74119* (FSU, VDB); Highlands, *Ray et al. 10370* (NCU, USF, VDB); Hillsborough, *Ray et al. 10126* (NCU, TAES, USF); Jackson, *Campbell 3770* (GH); Jefferson, *Campbell 3843* (GH); Lee, *Lakela et al. 30541* (NCU, USF); Liberty, *Campbell 4075* (GH); Martin, *Campbell 3896* (GH); Pasco, *Ray 9607* (GH, NCU, US, USF); Pinellas, *Tracy 7375* (MO, NY, W); Wakulla, *Godfrey 67525* (FSU, NCU, VDB); Walton, *Godfrey 55249* (DUKE, FSU, GA, GH, NY). MICHIGAN: Allegan, *Van Schaack s.n.,* 1945 (US); Berrien, *Parmelee 3017* (WIS); Livingston, *Kilburn 371* (MICH); Muskegon, *Bourdo 20* (MICH); Washtenaw, *Bartlett s.n.,* 1956 (MICH). OHIO: Athens, *Silby s.n.,* 1896 (NY); Cuyahoga, *Jones 1397* (TENN); Greene, *Demaree 11850* (MO, WIS); Hamilton, *Stephenson s.n.,* 1930 (GA, MO); Huron, *Jones 1270* (FSU, NCU); Pike, *Crowl s.n.,* 1937 (NY); Stark, *Brown s.n.,* 1940 (NY). INDIANA: Crawford, *Deam 30268* (US); Dariess, *Deam 7623* (US); Dearborn, *Deam 42717* (US); Franklin, *Deam 35304* (US); Lawrence, *Kriebel 1428* (DUKE); Monroe, *Duncan 271* (GA); Owen, *Deam 35013* (US); Pike, *Deam 35076* (MICH); Switzerland, *Deam 41098* (US). KENTUCKY: Bath, *Gleason & Griffiths G509b* (MICH); Butler, *Nicely 3136* (NCU); Kenton, *Braun 3752* (NY, US); Lincoln, *Wharton G584* (MO); Montgomery, *Wharton 6191* (MICH, MO, NY); Powell, *Gleason & Griffiths G173a* (MICH, NY, TENN). TENNESSEE: Blount, *Thomas s.n.,* 1965 (TENN); Coffee, *DeSelm 1994* (TENN); Fayette, *DeSelm s.n.,* 1972 (TENN); Graniger, *Cain s.n.,* 1938 (FSU, TENN, WIS); Knox, *Ruth 751* (NY); Monroe, *Sharp et al. 17048* (NCU, TENN); Morgan, *Rogers et al. 40973* (NCU, TENN); Polk, *Biltmore 21*^{b} (NY, W); Roane, *DeSelm 29898* (TENN); Washington, *Armentrout s.n.*, 1961 (TENN); White, *DeSelm 216* (TENN). ALABAMA: Baldwin, *Campbell 3803a* (GH); Covington, *Kral 44748* (VDB); Houston, *Campbell 4155* (GH); Lauderdale, *Kral 29355* (GA, TENN, VDB); Lee, *Earle 4* (MO, NY); Mobile, *Mohr s.n.*, 1884 (NY, US); Montgomery, *Campbell 3956* (GH); Randolph, *Campbell 4149* (GH); Sumter, *Campbell 3955* (GH). MISSISSIPPI: Bolivar, *Ray 5990* (MISSA, USF); Covington, *Jones 10878* (MISS); Forrest, *Rogers & Robbins 4885* (NCU, VDB); Harrison, *Tracy 4698* (GH, MISS, MO, NCU, W); Jackson, *Tracy 3787* (MO, NY); Lafayette, *Pullen 641532* (GA, MISS, NCU); Lamar, *Jones 2545* (FSU, MISS, NCU); Oktibbena, *Tracy 1398* (MO, NY); Pearl River, *Sargent 8489* (MICH, MISS, US); Tishomingo, *Ray 7560* (MISSA, NCU, USF, VDB (2 sheets)). ILLINOIS: Jackson, *Bailey & Swayne* (NCU); Lawrence, *Henderson 62-1056* (FSU); Pike, *Evers 67516* (NCU); Williamson, *Voigt s.n.*, 1950 (NCU). IOWA: Wapello, *Hayden 8446* (US). MISSOURI: Boone, *Rickett 1137* (DUKE); Butler, *Eggert s.n.*, 1893 (MO); Cape Girardeau, *Steyermark 64022* (MO); Franklin, *Croat 3912* (MO); Howell, *Steyermark 20034* (MO); Madison, *Steyermark 1433* (MO); New Madrid, *Steyermark 83438* (GA); Shannon, *Redfearn et al. 844* (NCU); St. Clair, *Henderson 67-1951* (FSU, VDB); St. Louis, *Steyermark 638* (MO). ARKANSAS: Baxter, *Robinson 2242* (NY); Benton, *Plank s.n.*, 1900 (MO); Calhoun, *Demaree 22670* (MO, NY); Clark, *Demaree 21760* (MO, NCU, US); Fulton, *Robinson 2285* (NY); Grant, *Demaree 16571* (MICH, MO, NY, US); Howard, *Demaree 9706* (MO, NY); Izard, *Robinson 2135* (NY); Jefferson, *Demaree 23398* (MO, NCU, NY); Miller, *Heller 4233* (MO, NY); Randolph, *Robinson 2310* (NY); St. Francis, *Demaree 59675* (NCU); Stone, *Robinson 2328* (NY). LOUISIANA: Allen, *Ball 233* (NY); Aroyelles, *Harvey 8099* (MICH); Beauregard, *Thieret 28136* (DUKE); Calcasieu, *Shinners 22124* (WIS); Jackson, *Thomas & Cicala 31821* (NCU, TENN); Lincoln, *Garrett 87* (WIS); Morehouse, *Thomas & DePoe 440* (VDB); Ouachita, *Thomas & Jones 895* (USF, VDB); Orleans, *Hooker s.n., s.d.* (NY); St. Tammany, *Arsène et al. 11151* (NY); Vermilion, *Reese 6083* (VDB). KANSAS: Neosho, *Holland 2593* (NCU); Wyandotte, *Henderson 64-628* (FSU). OKLAHOMA: Bryan, *Taylor 7176* (VDB); Cleveland, *Nighswonger N-316* (TAES); Delaware, *Wallis 5945* (FSU, NCU, VDB); Le Flore, *Waterfall 15223* (GH); McCurtain, *Rickerson 447* (USF); Ottawa, *Wallis 8369* (FSU, NCU, VDB); Payne, *Bridge 220* (USF); Sequoyah, *Wallis 5640* (VDB). TEXAS: Angelina, *McCall 64-30* (TAES); Aransas, *Cory 51161* (MICH, NY); Bowie, *Letterman s.n.*, 1894 (MICH, MO, NY); Dallas, *Kral 447* (FSU); Ft. Bend, *Silveus 5429* (TAES); Galveston, *Waller & Bauml 3284* (GH, TAES); Gonzales, *Tharp et al. s.n.*, 1948 (DUKE, NY); Houston, *Coleman s.n.*, 1935 (TAES); Montgomery, *Gould 5399* (TAES); Newton, *Parker & Cory 10861, 10862* (TAES); Robertson, *Gould 6556* (TAES); San Jacinto, *Hartman 1280.5* (TAES); Smith, *Reverchou 2206* (MO, NY); Titus, *McGregor 706* (WIS); Tyler, *Gould 7308* (TAES); Waller, *Silveus 5118* (TAES). CALIFORNIA: Calaveras, *Bacigalupi 6087* (UC); Placer, *Crampton 5793* (TAES); Sacramento, *Crampton 5129* (TAES); Sonoma, *Yates 6865* (MO); Stanislaus, *Crampton 3025* (TAES). HAWAII: Oahu, *Correll 12307* (GH). **Mexico.** SAN LUIS POTOSÍ, *Schaffner 1049* (GH). VERACRUZ: Jalapa, *Hitchcock 274* (GH, TEX, UC, W). OAXACA: Tolusa[?], *Beetle et al. M-1362* (FLAS). CHIAPAS: La Trinitaria, *Breedlove 36962* (CAS). QUINTANA ROO: Laguna Chemkabnab, *Swallen 2771* (MICH). **Belize:** Boomtown, *O'Neill 8466* (CAS, F, GH, MICH, UC); Manatee Lagoon, *Peck 150* (GH). MORAZÁN: El Jicarito Region, *Standley 24241* (F, UC); Quebrada de Santa Clara, *Standley 22300* (F, MICH). **Guatemala.** HUEHUETENANGO: Finca San Rafael, *Steyermark 49490* (F); Miramar, *Steyermark 51535* (F). **Honduras:** Morazán, 87°W, 14°N, *Williams & Molina 17173* (GH). **Nicaragua.** MANAGUA, *Garnier 1951a* (GH). **Panama.** CANAL ZONE, *Hitchcock 8013* (CAS, MICH). PANAMÁ: Chorrera, *Hitchcock 8143* (MICH). **Bermuda:** without further locality, *Brown & Britton 225* (GH). **Greater Antilles.** CUBA. Pinar del Río: Herradura, *Ekman 14081* (US); Remartes, *Ekman 11370* (US); San Diego de los Baños, *León 5118* (GH); San Felipe, *León 15862* (GH); San Julian, *Ekman 11140* (MICH). Isla de Pinos: Los Indios, *León & Victorin 17868* (GH, US). Las Villas: Helechales, *León 5407* (GH); Soledad, *Jack 6193* (A, CAS). Oriente: Loma Mensara, *Ekman 3211* (TEX, US). JAMAICA: Appleton, *Hitchcock 9656½* (US); Bull Head Mtn., *Hitchcock 9542* (US); Cinchona, *Harris 11268* (GH, US); Claremont, *Hitchcock 275* (GH, TEX, W); Montego Bay, *Hitchcock 9680*

(US). DOMINICAN REPUBLIC: Monte Cristi, *Ekman 12771* (GH, TEX); Santo Domingo, Trujillo, *Allard 13194* (GH). **Lesser Antilles.** TRINIDAD AND TOBAGO: *Broadway 4044* (GH). **Colombia.** CHOCÓ: near Quidbo, *Gentry & Renteria 24517* (MO). **Japan.** KYUSHU: Hondo, *Togasi s.n.,* 1952 (GH, W, WIS).

This variant is named for its prominence in old-field succession in the eastern United States. The type in the Linnaean herbarium apparently represents one part of this variant, and it is the basis of the common concept of *Andropogon virginicus.* The variant includes two kinds of plants that are so close they cannot be distinguished either in the field or in the herbarium with great confidence, although their extremes differ somewhat in height, inflorescence thickness, and number of racemes per inflorescence unit. I have seen the two kinds growing together in northern Florida and in North Carolina, where they are barely distinguishable.

The deceptive variant may also closely resemble the old-field variant. The former has narrower raceme sheaths and a peduncle that occasionally exceeds 10 mm in length. These two variants are more easily separated in the field than the two kinds of plants of the old-field variant, but a similar uncertainty about herbarium material still prevails.

7a. 2. **Deceptive variant** FIGURES 11, N; 42.

DIAGNOSIS. Raceme sheaths narrow; peduncles sometimes greater than 10 mm long; racemes usually 2.

DISTRIBUTION. Flatwoods, scrublands, disturbed sites (e.g., cleared timberlands). Coastal Plain from North Carolina to Florida (MAP 16).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA: Isle of Wight, *Fernald & Long 12568* (GH, US); Nansemond, *Fernald & Long 10943* (DUKE, GH, US). NORTH CAROLINA: Bertie, *Campbell 4223* (GH); Bladen, *Campbell 4208* (GH); Dare, *Fosberg 17875* (MICH); Duplin, *Blomquist & Correll 4819* (GH); Martin, *Radford 41798* (WIS); Nash, *Godfrey & Kerr 6621* (DUKE). SOUTH CAROLINA: Beaufort, *Cuthbert s.n.,* 1886 (FLAS); Berkeley, *Ahles 35450* (NCU); Clarendon, *Campbell 4222* (GH); Jasper, *Bell 4813* (NCU). GEORGIA: Brantley, *Campbell 4229* (GH); Calhoun, *Thorne 6903* (GH); Clinch, *Eyles 397* (MO); Long, *Bozeman 1944* (GA); McIntosh, *Duncan 20643* (WIS); Thomas, *Campbell 3922* (GH), Tift, *Shepherd 341* (TAES). FLORIDA: Alachua, *Campbell 4186* (GH); Baker, *Godfrey 74698* (FSU); Bay, *Billington s.n.,* 1921 (MICH); Brevard, *Fredholm 6193* (US); Calhoun, *Godfrey 75791* (FSU); Charlotte, *Lakela 24675* (FLAS, GH); Clay, *Swallen 5583, 5598, 5614* (US); Collier, *Lakela 31155* (GA, USF); Dade, *Silveus 6620* (DUKE); Duval, *A. H. Curtiss 3639d* (GH); Franklin, *Campbell 3931* (GH); Gulf, *Chapman s.n., s.d.* (GH); Highlands, *Campbell 3747* (GH); Hillsborough, *Lakela 26662* (GH); Indian River, *Tracy 9257* (TAES, US); Jackson, *Campbell 4081* (GH); Jefferson, *Campbell & Godfrey 4068* (GH); Lake, *Campbell 4197* (GH); Lee, *Hitchcock 441* (MO); Leon, *Godfrey & Campbell 4230* (GH); Liberty, *Campbell et al. 4168* (GH); Manatee, *Tracy 7107* (MO, NY, W); Martin, *Campbell 3870* (GH); Nassau, *Godfrey 74699* (FLAS); Okeechobee, *West 23* (FLAS); Pinellas, *Davis s.n., s.d.* (FLAS); Polk, *Lakela 23585* (GH, US); Putnam, *Godfrey 76896* (FSU); St. Lucie, *Silveus 6665* (TAES); Sarasota, *McFarlin & Van Dyne 12037* (US); Seminole, *Chase 4137* (US); Walton, *Godfrey 75763* (FSU).

This variant is so named because of its deceiving similarity to three other taxa, the old-field variant of *Andropogon virginicus* var. *virginicus, A. glomeratus* var. *hirsutior,* and the robust variant of *A. glomeratus* var. *pumilus.*

Maps 13–16. Distribution of some subspecific taxa of *Andropogon virginicus*: 13, var. *glaucus*, wetlands variant; 14, var. *glaucus*, drylands variant; 15, var. *virginicus*, smooth variant; 16, var. *virginicus*, deceptive variant.

Discussion of the distinguishing characteristics of the deceptive variant is provided under each of these taxa.

The deceptive variant does not correspond to any taxon for which a name has been published. Its discovery has been crucial to an understanding of

Andropogon virginicus because the variant appears to be both the primitive member of the species and the evolutionary link to *A. brachystachyus.*

7a. 3. **Smooth variant** FIGURE 48.

DIAGNOSIS. Like old-field variant but with glaucous stems and glabrous leaves.

DISTRIBUTION. Poorly drained soils (e.g., shallow ponds, swales, cut-over flatwoods); much less common than old-field variant. Coastal Plain from North Carolina to Mississippi (MAP 15).

REPRESENTATIVE SPECIMENS. **United States.** NORTH CAROLINA: Bladen, *Campbell 4213* (GH). GEORGIA: Brantley, *Campbell 4202* (GH); Wayne, *Campbell 4228* (GH). FLORIDA: Alachua, *Campbell 4232* (GH); Brevard, *Fredholm 6109* (GH, US); Franklin, *Godfrey 77363* (FSU); Gulf, *Chapman s.n., s.d.* (GH); Highlands, *Campbell 3902* (GH); Indian River, *Tracy 9759* (TAES); Jackson, *Campbell 3785* (GH); Leon, *Godfrey 74595* (FSU, VDB); Liberty, *Godfrey 75790* (FSU); Martin, *Campbell 4129* (GH); St. Johns, *Campbell 4227* (GH); Volusia, *Silveus 6736* (TAES); Wakulla, *Godfrey & Morar 61570* (FSU); Walton, *Campbell 3787* (GH). ALABAMA: Baldwin, *Campbell 3803b* (GH). MISSISSIPPI: Jackson, *Tracy 2276* (NY).

The smooth variant does not correspond to any taxon for which a name has been published. It is a glaucous-stemmed, glabrous-leaved derivative of the old-field variant that has a narrower tolerance for soil moisture conditions. From a limited number of observations of progeny of these two taxa, there is no evidence that they are genetic segregates of one another.

7b. **Andropogon virginicus** L. var. **glaucus** Hackel in DC. Monogr. Phanerog. **6:** 411. 1889. TYPE: Florida, Duval County, *A. H. Curtiss 3638b* (holotype, W!; isotypes, GA (two sheets)!, GH!, MISSA!, MO!, US!).

FIGURES 11, O; 42; 43; 47.

Andropogon virginicus L. var. *dealbatus* Hackel[8] in DC. Monogr. Phanerog. **6:** 411. 1889. TYPE: Alabama, Mobile County, *Mohr 1884* (holotype, W!).

Andropogon capillipes Nash, Bull. New York Bot. Gard. **1:** 431. 1900. Based on *Andropogon virginicus* L. var. *glaucus* Hackel. Not *Andropogon glaucus* Retz., 1789, or *Andropogon glaucus* Muhl., 1817.

DIAGNOSIS. Leaves glaucous; racemes 2, rarely 3.

DISTRIBUTION. Moist or dry soils on Coastal Plain. Southern New Jersey to eastern Texas (MAPS 13, 14).

The diagnoses and distributions of the drylands and wetlands variants of this taxon are included in the comparative discussion of the two taxa.

REPRESENTATIVE SPECIMENS.

Drylands variant. **United States.** NORTH CAROLINA: Brunswick, *Blomquist 10442* (DUKE); New Hanover, *Chase 4582* (US). SOUTH CAROLINA: Allendale, *Campbell 4015* (GH). GEORGIA: Brantley, *Campbell 4025* (GH); Echols, *DeSelm 1969* (TENN); Ware, *Campbell*

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[8] Hackel's *Andropogon virginicus* L. vars. *glaucus* and *dealbatus* are united here for the first time. The former varietal name is used here to preserve common usage.

3708 (GH); Wayne, *Campbell 4020* (GH). Florida: Bay, *Godfrey 76131* (FSU); Brevard, *Fredholm 6128* (GH, MO, US); Calhoun, *Ford 5642* (FLAS, NCU, W); Citrus, *DeSelm 1969* (TENN); Collier, *Lakela 31192* (GH, MO, NCU); Columbia, *Silveus 6749* (DUKE, GA, TAES); Dade, *Silveus 5284* (TAES, VT); DeSoto, *DeSelm s.n.*, 1969 (TENN); Dixie, *Godfrey 56152* (FSU, GH, NY, USF); Duval, *A. H. Curtiss 36386* (GA, GH, MISSA, MO, US); Franklin, *Godfrey 74585* (FSU, NCU, VDB); Glades, *McCart 11190* (USF); Gulf, *Silveus 6742a* (GA, TAES, US); Hamilton, *Godfrey 74648* (FSU, NCU, VDB); Highlands, *Brass 15632* (GH, US); Hillsborough, *Lakela 23614* (US, USF); Jackson, *Campbell et al. 4165* (GH); Jefferson, *Godfrey 75828* (FSU); Lafayette, *Godfrey 76906* (FSU); Lake, *Ray 10543* (GH, US); Lee, *Stanley 12536* (US); Liberty, *Campbell 3827* (GH); Marion, *Campbell 4196* (GH); Martin, *Campbell 3898* (GH); Okaloosa, *Godfrey 68900* (FSU); Okeechobee, *McCart 11120* (USF); Orange, *Anderson 4085* (FSU); Osceola, *Campbell 3865* (GH); Palm Beach, *Davis s.n.*, 1941 (GH); Pinellas, *Tracy 7377* (GH, MO, NY, TAES, US, W, WIS); St. Johns, *Godfrey 74716* (FSU); St. Lucie, *Silveus 6660* (TAES, US); Seminole, *Beardslee 43* (US); Wakulla, *Godfrey 74591* (FLAS, FSU, NCU, VDB). Alabama: Baldwin, *Kral 38250* (GA, VDB); Covington, *Kral 44730* (VDB).

Wetlands variant. **United States.** New Jersey: Cape May, *Long 5145* (NY). North Carolina: Bladen, *Ashe s.n., s.d.* (NCU, NY); Brunswick, *Blomquist 405* (DUKE, NY); Cumberland, *Ahles 36571* (NCU). Georgia: Bullock, *Campbell 4018* (GH); Colquitt, *Godfrey 76085* (FSU); Harris, *Jones 22259* (GA); Long, *Bozeman & Radford 1943* (NCU). Florida: Bay, *Godfrey 76135* (FSU); Bradford, *Conde s.n.*, 1977 (FLAS); Charlotte, *DeSelm s.n.*, 1969 (TENN); Clay, *Campbell & Godfrey 4136* (GH); Collier, *Cooley et al. 9062* (FSU, GH, USF); Columbia, *Ashe s.n.*, 1929 (NCU); Dixie, *Godfrey 69228* (FSU); Duval, *A. H. Curtiss 6055* (GH, TAES); Escambia, *Silveus 6756* (TAES, VT); Gulf, *Chapman s.n., s.d.* (GH, MO, NY); Hillsborough, *Combs 1346a* (US); Indian River, *Tracy 9284* (TAES, US); Jackson, *Campbell 3912* (GH); Lee, *Wunderlin et al. 5399* (USF); Leon, *Godfrey 75786* (FSU); Liberty, *Campbell 3820* (GH); Pasco, *Ray 9596* (USF); Putnam, *Godfrey 74721* (FSU, NCU, VDB); Santa Rosa, *Godfrey 76185* (FSU); Walton, *Campbell 3940* (GH); Wakulla, *Godfrey & Morar 61570a* (DUKE, FLAS, FSU, USF); Washington, *Campbell 3938* (GH). Alabama: Baldwin, *Campbell 3800* (GH); Butler, *Kral 44702* (VDB); Geneva, *Kral 41714* (GH, USF, VDB); Mobile, *Mohr s.n.*, 1884 (NY, US, W). Mississippi: Forrest, *Rogers & Robbins 4884-B* (MISS); Harrison, *Tracy 3897* (MO, NY, TAES); Jackson, *Tracy 3814* (TAES). Louisiana: Calcasieu, *Thieret 27991* (FSU); Livingston, *Rogers 2419-A* (MISS, NCU); Rapides, *Duvall 6019* (TAES); St. Mary, *Silveus 5406* (TAES). Texas: Galveston, *Waller 3316* (GH, TAES); Houston, *Lindheimer s.n.*, 1841 (MO).

The pattern of small morphological differences associated with ecological differences of *Andropogon virginicus* var. *virginicus* reappears in the pair of taxa comprising *A. virginicus* var. *glaucus*. The drylands variant of *A. virginicus* var. *glaucus* produces generally shorter raceme sheaths, racemes, and spikelets; its flowers are more frequently chasmogamous, and unlike the wetlands variant, it has no hairs below the raceme sheath. In addition, it grows in better-drained soil and has a narrower geographic range.

In the majority of instances, these morphological and soil-moisture differences are correlated. I have seen these taxa growing within one to three meters of one another at three localities in northwestern Florida. At only one of these was there difficulty in classifying any individual: a single plant on a slope between a bog inhabited by the wetlands variant and a roadside lined with the drylands variant combined the morphological features of these two taxa. The cause of this morphological intermediacy is unknown.

The strong overlap in the characters separating the drylands and wetlands variants and the breakdown in the correlation of these characters in about five percent of all populations examined in the herbarium are the reasons these two taxa are not recognized nomenclaturally.

Hackel (1889) suggested that the drylands variant of *Andropogon virginicus* var. *glaucus* is closely related to ("vergit ad") *A. brachystachyus.* In inflorescence morphology the two are sometimes similar because larger plants of the drylands variant usually produce arching branches (FIGURE 43); they also share a preference for well-drained soils. They differ in stem height, in glaucousness, in peduncle, spikelet, and anther length, and in anther color. It is possible that *A. brachystachyus* stock is ancestral to the drylands variant, but the deceptive variant of *A. virginicus* var. *virginicus* is a more likely ancestor of the drylands variant because there is an even closer resemblance between these two. Apart from glaucousness, they differ in raceme-sheath length and in pubescence below the raceme sheath.

Since the deceptive and wetlands variants differ from the drylands variant in the same characters, it is not surprising that the first two taxa are morphologically alike. In addition to glaucousness, the wetlands variant differs from the deceptive variant in its larger raceme sheaths, wider range, and tolerance of more soil moisture.

Leaves of the wetlands variant are sometimes faintly glaucous, even on healthy plants. If such plants are not examined carefully, they may be mistaken for a plant of the smooth variant with inflorescence units with only two racemes.

8. **Andropogon brachystachyus** Chapman, Fl. So. U. S. ed. 2. 668. 1883. TYPE:[9] Florida, Duval County, *A. H. Curtiss 3632* (lectotype, US!; isolectotypes, DUKE!, FSU!, GA!, GH!, MO (two sheets)!, NCU!, US!). *Sorghum brachystachyum* (Chapman) Kuntze, Rev. Gen. Pl. **2:** 791. 1891. *Anatherum brachystachyum* (Chapman) G. Roberty, Boissiera **9:** 212. 1960.
FIGURES 11, G; 44; 47.

DIAGNOSIS. Stems tall; leaves long, sparsely pubescent; inflorescence branches long, arching (in herbarium specimens inflorescences appear rather open); racemes and awns short; spikelets and anthers long.

DISTRIBUTION. Sandy, often seasonally wet soils of flatwoods, savannas, pond margins, and scrublands. Southern Georgia and Florida (MAP 3).

REPRESENTATIVE SPECIMENS. **United States.** GEORGIA: Brantley, *Campbell 4022* (GH); Chatham, *Eyles 6652* (US); Long, *Bozeman 1908* (NCU); Wayne, *Campbell 4021* (GH). FLORIDA: Alachua, *Silveus 6519* (TAES, US); Baker, *Ashe s.n.*, 1928 (NCU); Brevard, *Fredholm 5558* (GH, MO, US); Clay, *Harper 40* (GH, MO, US); Collier, *Lakela 30327* (GH, NCU, NY, USF); Columbia, *DeSelm s.n.*, 1969 (TENN); Dixie, *Godfrey 56183* (FSU, GA, GH, USF); Duval, *A. H. Curtiss 5338* (GA, GH, US); Highlands, *Campbell 3884* (GH); Indian River, *Tracy 9285* (TAES, US); Jefferson, *Godfrey 74602* (FSU, NCU, VDB); Lafayette, *Godfrey 74632* (FSU, VDB); Lake, *Nash 1193* (GH, MO, NY, TAES, US); Leon, *Godfrey 74594* (FSU, VDB); Levy, *Godfrey et al. 64751* (FSU, VDB); Madison, *Godfrey 75831* (FSU); Marion, *Campbell 4195* (GH); Martin, *Campbell 3897* (GH); Nassau, *Godfrey 74680* (FSU, NCU, VDB); Okeechobee, *McCart 11121* (USF); Orange, *Baker 39* (GH, NY); Osceola, *Campbell*

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[9] The lectotypification of Hitchcock (1951) is followed here.

3864 (GH); Pasco, *Ray 9588* (GH, NCU, USF, VDB); Pinellas, *Tracy 7376* (GH, MO, NY, TAES, US); Polk, *Lakela 23584* (US, USF); Putnam, *Godfrey 74720* (FSU, NCU); Seminole, *Beardslee 46* (US); St. Johns, *Godfrey 74719* (FSU, NCU, VDB); Taylor, *Godfrey 74634* (FSU, NCU, VDB); Volusia, *Hood 65* (US).

The combination of elongate, arching inflorescence branches, long peduncles, and short racemes makes *Andropogon brachystachyus* very distinctive. Its closest relative is the deceptive variant of *A. virginicus* var. *virginicus.* These two taxa are separated by a morphological distance of 8 (TABLE 6). The deceptive variant may be a cleistogamous derivative of ancestral stock of *A. brachystachyus.*

One population of *Andropogon brachystachyus* in Long County, Georgia (*Campbell 4021*), on the northern edge of this taxon's range, suggests that one of its ancestors might have given rise to the deceptive variant. Most of the plants in this population are characteristic of *A. brachystachyus*: they are tall (average, 2 m; range, 1.57–2.17 m); the branches arch; the peduncles range from 20 to 40 mm long; the spikelets exceed 4 mm in length; and the anthers are more than 1.9 mm long. Two individuals, however, are shorter (average, 1.4 m) and have erect to only slightly arching branches, peduncles less than 13 mm, spikelets less than 3.8 mm, and anthers less than 1.4 mm. As peduncle, spikelet, and anther length suggest, there is a greater frequency of cleistogamous flowers at the base of the racemes of these two individuals than in the rest of the population. These changes may be the product of mutation in regulatory genes hastening sexual maturity. The importance of these plants is that they are strikingly similar to the deceptive variant of *A. virginicus* var. *virginicus.* Because of its smaller size, erect branches, shorter peduncles, and longer racemes, the deceptive variant has a much different appearance than plants of *A. brachystachyus* (except the anomalous individuals of the Long County population). In less conspicuous ways, however, they are very alike. They have the same ligule morphology, amount and distribution of leaf pubescence, and stem internode color. They differ, however, in three nonmorphological ways. First, in peninsular Florida the deceptive variant flowers two to four weeks before *A. brachystachyus,* although at the northern limit of the range of *A. brachystachyus,* their flowering periods overlap. Second, the deceptive variant is more frequently cleistogamous. Third, *A. brachystachyus* may form large, dense populations, but it does not invade disturbed sites as does the deceptive variant. It seems plausible that the deceptive variant arose from *A. brachystachyus* stock as a precociously flowering form. This paedomorphosis (Gould, 1977) may be reflected in the earlier flowering time of the deceptive variant and, through the introduction of cleistogamy, may have provided the deceptive variant with a breeding system that is adaptive for a colonizer.

9. **Andropogon glomeratus** (Walter) B.S.P. Prelim. Catal. Anthophyta Pteridophyta New York, 66. 1888. Based on *Cinna glomerata* Walter, Fl. Carolin. 59. 1788. TYPE: South Carolina (holotype, BM, not seen; fragment, NY!; photo, GH!). *Sorghum glomeratum* (Walter) Kuntze, Rev. Gen. Pl. **2:** 790. 1891. *Anatherum virginicus* (L.) Sprengel subvar. *glomeratus* (Walter) G. Roberty, Boissiera **9:** 212. 1960.

Andropogon macrourus Michaux, Fl. Bor. Am. 56, 57. 1803, *nomen superfl.* for *Cinna glomerata* Walter and with same type. *Andropogon spathaceus* Trin. Fund. Agrost. 186. 1820, *nomen nudum,* placed in synonymy of *Andropogon macrourus* Michaux by Steudel, Nomencl. Bot. ed. 2. **1:** 93. 1840. *Anatherum macrourum* (Michaux) Griseb. Mem. Am. Acad. II. **8:** 534. 1864, as *macrurum. Dimeiostemon macrourus* (Michaux) Jackson, Index Kew. **1:** 760. 1893, *pro syn.,* as *macrurum.*

DIAGNOSIS. Stem sheaths scabrous (smooth in taxon 9c, often in 9d); leaf blades long; ligules long, light brown, short-ciliate (often short and with long ciliations in taxon 9d); inflorescences oblanceolate to obpyramidal, usually with at least 3 branches at 1 or more stem nodes; inflorescence units numerous.

DISTRIBUTION. Poorly drained soils; throughout entire range of virginicus complex. Only *Andropogon glomeratus* var. *pumilus* extends beyond eastern United States to western United States, Mexico, Central America, West Indies, and South America.

Of the five taxa included in *Andropogon glomeratus,* three (vars. *glomeratus, hirsutior,* and *glaucopsis*) are particularly close to one another morphologically and ecologically. Besides the characters given in the species diagnosis, these three varieties have ligules that are identical in their length, short-ciliate margins, and color. *Andropogon glomeratus* var. *glomeratus* appears to be the most primitive of the three because of its frequent chasmogamous flowering (as expressed in the long peduncles and large anthers). It also generally has larger spikelets than the mostly cleistogamous vars. *hirsutior* and *glaucopsis.* Finally, inflorescence shape can be used to separate var. *glomeratus* from the other two taxa. Although the distance between vars. *glomeratus* and *hirsutior* is only 4 (TABLE 6), the characters separating them are usually consistent and clear.

In Virginia and the Carolinas, where individuals of vars. *glomeratus* and *hirsutior* may infrequently have similar peduncle lengths, one must rely upon inflorescence shape, spikelet and anther length, and flowering mode for identification.

While the stem sheaths of vars. *glomeratus* and *hirsutior* are scabrous, pubescent (at least near the collar), and green, those of var. *glaucopsis* are smooth, glabrous, and glaucous. Glaucousness (uncommon in the complex, in sect. LEPTOPOGON, and in the genus as a whole) is the basis for the conjecture that var. *glaucopsis* is derived, probably from var. *hirsutior* stock. FIGURE 49 shows the hypothesized phylogeny of these three taxa.

The greatest problem within *Andropogon glomeratus* is the affinity of the robust variant of var. *pumilus.* In the past either it has not been recognized or it has been given the status of species, variety, or form. Morphologically, it is clearly farther from any of the first three taxa of the species than each of these is from any other. As discussed for vars. *glomeratus* and *hirsutior,* the robust variant may often appear very similar to them in general appearance. Characters of stem-sheath and glume-keel scabrousness and ligule morphology distinguish the robust variant and place the southwestern variant of var. *pumilus* in between the robust variant and the rest of *A. glomeratus.* The morphological inter-

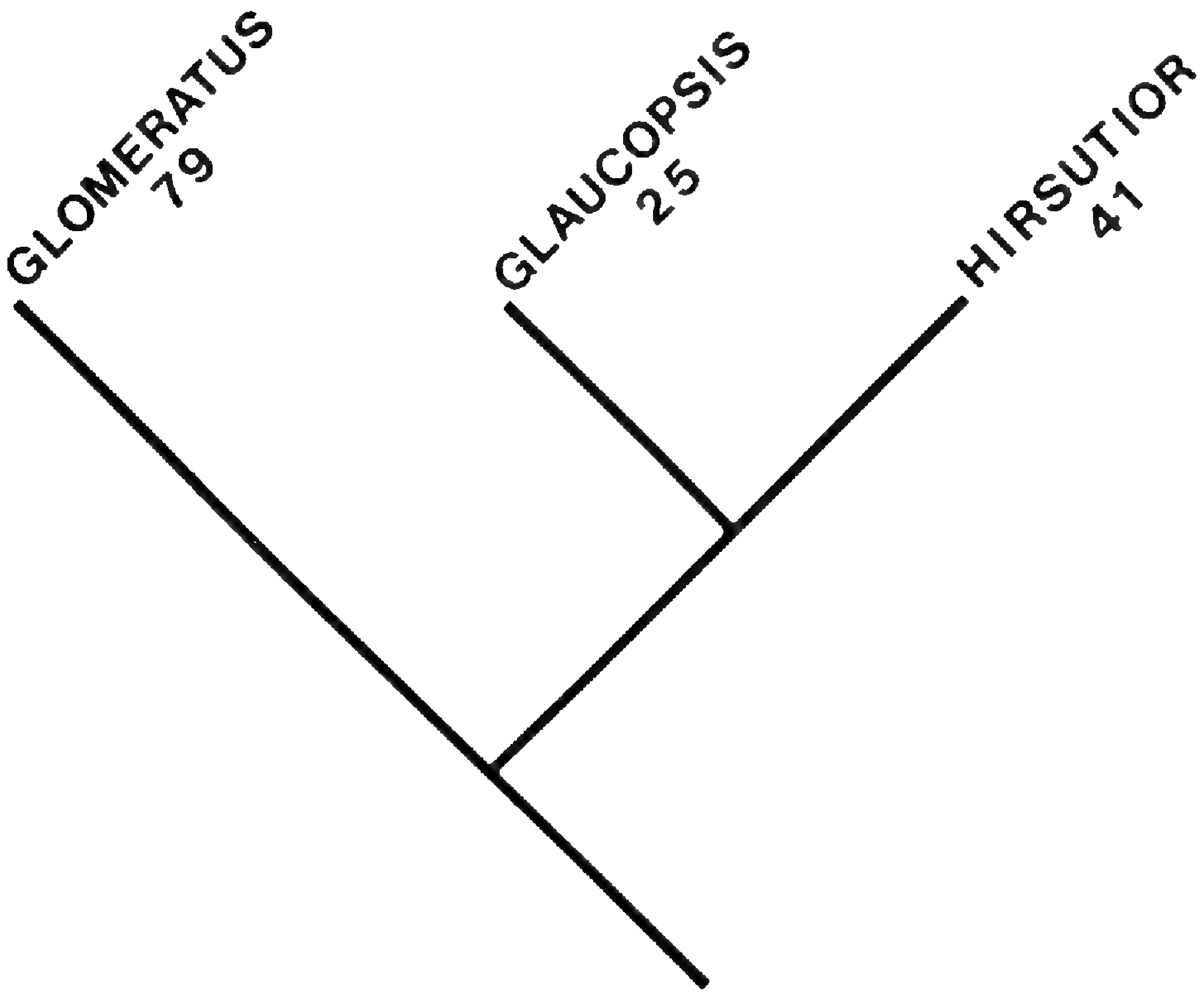

FIGURE 49. Hypothesized phylogeny of *Andropogon glomeratus* vars. *glomeratus*, *hirsutior*, and *glaucopsis*. Numbers below names indicate mean percent chasmogamy (character 33 of TABLE 6).

mediacy of the southwestern variant unites the robust variant and vars. *glomeratus*, *hirsutior*, and *glaucopsis*.

Key to the Subspecific Taxa of *Andropogon glomeratus*

1. Leaves glaucous. .... 9c. *A. glomeratus* var. *glaucopsis*.

1. Leaves green.
    2. Raceme sheaths usually less than 2.5 mm wide; stem sheaths often smooth; ligules usually less than 1 mm long, often with long-ciliate margins. .... 9d. 1. Robust variant of *A. glomeratus* var. *pumilus*.
    2. Raceme sheaths usually more than 2.5 mm wide; stem sheaths often rough; ligules usually more than 1 mm long, with short-ciliate margins.
        3. Keels of lower glume scabrous to well below middle; plants of southwestern United States and northwestern Mexico. .... 9d. 2. Southwestern variant of *A. glomeratus* var. *pumilus*.
        3. Keels of lower glume scabrous only above middle; plants of eastern United States.
            4. Inflorescences (linear-)oblong; spikelets usually less than 4 mm long; anther usually marcescent within spikelet; peduncles less than 10 mm long; plants of Coastal Plain from Maryland to Mississippi. .... 9b. *A. glomeratus* var. *hirsutior*.
            4. Inflorescences oblong to obpyramidal; spikelets usually more than 4 mm long; anther usually not marcescent within spikelet; usually some mature

peduncles more than 10 mm long; plants of Coastal Plain and well inland from Massachusetts to Mississippi. . . 9a. *A. glomeratus* var. *glomeratus.*

9a. **Andropogon glomeratus** (Walter) B.S.P. var. **glomeratus**

Figures 11, S; 53.

Andropogon macrourus Michaux var. *abbreviatus* Hackel in DC. Monogr. Phanerog. **6:** 408. 1889. Type:[10] Carolina, *Rugel s.n.,* 1841 (lectotype, W!). *Andropogon glomeratus* (Walter) B.S.P. var. *abbreviatus* (Hackel) Scribner, U. S. D. A. Div. Agrost. Bull. 7(ed. 3): 15. 1900. *Andropogon corymbosus* (Hackel) Nash var. *abbreviatus* (Hackel) Nash in Britton, Man. Fl. No. States Canada, 70. 1901.

Andropogon macrourus Michaux var. *corymbosus* Hackel in DC. Monogr. Phanerog. **6:** 409. 1889. Type: Florida, Duval County, *A. H. Curtiss 3639c* (holotype, W!; isotypes, FLAS!, GH (2 sheets)!, NCU, US!) (*N.B.: Curtiss 3639c* of GA! and MISSA! are taxon 9d). *Andropogon glomeratus* (Walter) B.S.P. var. *corymbosus* (Hackel) Scribner, U. S. D. A. Div. Agrost. Bull. 7(ed. 3): 15. 1900. *Andropogon corymbosus* (Hackel) Nash in Britton, Man. Fl. No. States Canada, 69. 1901. *Andropogon virginicus* L. var. *corymbosus* (Hackel) Fern. & Griscom, Rhodora **37:** 142. 1935.

Diagnosis. Inflorescences oblong to obpyramidal; peduncles and spikelets usually long; stamens not regularly marcescent within spikelets.

Distribution. Bogs, swamps, savannas, flatwoods, and ditches. Massachusetts to Kentucky and Arkansas, south to Florida and Louisiana (Map 17).

Representative specimens. **United States.** Massachusetts: Barnstable, *Fernald et al. 14984* (GH); Bristol, *Sturtevant s.n.,* 1888 (MO); Dukes, *Seymour 1441* (DUKE, GH, NY); Nantucket, *William s.n.,* 1894 (GH); Plymouth, *Blake 11425* (MICH, US). Rhode Island: Washington, *Collins & Lownes s.n.,* 1923 (GH). New York: Nassau, *Bicknell 9643* (NY); Richmond, *Britton s.n.,* 1879 (NY); Suffolk, *Smith 3495* (MO, WIS). New Jersey: Atlantic, *Letterman s.n.,* 1887 (MICH, MO); Burlington, *MacElwee 1571* (GH, MO, NY); Camden, *Stewart 3052* (NY); Gloucester, *Fosberg 14488* (DUKE); Middlesex, *Miller 1077* (NY); Monmouth, *Britton s.n.,* 1883 (NY); Ocean, *Morton 40931* (VDB); Passaic, *Nash s.n.,* 1899 (NY). Pennsylvania: Berks, *Brumbach 353-34* (GH); Chester, *Pennell 8890* (NY); Fayette, *Boardman s.n.,* 1941 (VT); Lancaster, *Carter s.n.,* 1910 (NY); Philadelphia, *Van Pelt s.n.,* 1906 (GH). Delaware: Kent, *Goodale 62538* (GH); Sussex, *Churchill s.n.,* 1908 (MO). Maryland: Baltimore, *Freeman s.n.,* 1874 (WIS); Harford, *Wilkins 5709* (GH); Howard, *Foreman s.n.,* 1873 (NY); Prince Georges, *True 2879* (DUKE, GA, US); Worcester, *Campbell 3983* (GH). District of Columbia: *Hitchcock 256* (GH, MO, NY, USF, W). West Virginia: Cabell, *Millendor s.n.,* 1939 (US); Raleigh, *Berkley 2253* (US). Virginia: Accomac, *Fernald et al. 5577* (GH); Appomattox, *Kral 11179* (NCU); Augusta, *Massey 3101* (NCU); Isle of Wight, *Fernald & Long 5759* (GH); James City, *Grimes 3874* (NY); Northampton, *Fernald & Long 5183* (GH); Southampton, *Campbell 4217* (GH); Surry, *Terrell 4368* (NCU). North Carolina: Allegheny, *Blomquist & Anderson 925* (DUKE); Bertie, *Ahles & Haesloop 52066* (NCU); Bladen, *Ahles 37431* (NCU); Brunswick, *Bartram s.n.,* 1922 (GH); Buncombe, *Biltmore 920*^{b} (MO, NCU, NY); Cherokee, *Radford 17577* (NCU); Chowan, *Ahles & Duke 51029* (NCU); Columbus, *Bell 15740* (NCU); Craven, *Godfrey & White 6835* (GH); Cumberland, *Ahles & Leisner 33534* (NCU); Currituck, *Blomquist 14382* (DUKE); Davidson, *Denke s.n.,* 1826 (DUKE); Gates, *Godfrey 7037* (GH); Halifax,

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[10] Hackel cited "New Jersey (Gray); South Carolina (Rugel)." The 1841 collection of Rugel from "Carolina" is here designated as the lectotype rather than Rugel's 1842 collection from "Carolina" (W!). I have not seen material of Gray from New Jersey that Hackel would have seen.

FIGURES 50–55. 50–54, inflorescences: 50, *Andropogon glomeratus* var. *hirsutior* (*Campbell 3851*); 51, robust variant of *A. glomeratus* var. *pumilus* (*Campbell 4030*); 52, southwestern variant of *A. glomeratus* var. *pumilus* (*Crampton 6710*, Yolo Co., California (UC)); 53, *A. glomeratus* var. *glomeratus* (*Campbell 3915*); 54, *A. glomeratus* var. *glaucopsis* (*Campbell 3812*). 55, *A. glomeratus* var. *glaucopsis* (*Campbell 3812*), basal clumps of leaves. Scale = 15 cm.

MAPS 17–19. Distribution of some subspecific taxa of *Andropogon glomeratus*: 17, var. *glomeratus*; 18, var. *hirsutior*; 19, var. *glaucopsis*.

Ahles & Leisner 20846 (FSU, NCU); Harnett, *Laing 381* (NCU); Henderson, *Hunnewell 10084* (GH); Hertford, *Ahles & Haesloop 52210* (NCU); Hoke, *Correll 7184* (DUKE, GH); Jackson, *Correll 7903* (DUKE); Johnston, *Radford 29217* (NCU); Jones, *Radford 40022* (NCU); Lee, *Stewart s.n.*, 1958 (NCU); Macon, *Anderson s.n.*, 1953 (DUKE, FSU, GH); Martin, *Radford 41831* (NCU); Moore, *Blomquist 277* (DUKE); Nash, *Ahles & Leisner 21259* (NCU, VDB); Onslow, *Wilder 17676* (DUKE); Orange, *Ashe s.n., s.d.* (NY); Pamlico, *Radford 42286* (NCU); Pender, *Wells s.n.,* 1925 (NY); Pitt, *Radford 41604* (NCU); Richmond, *Radford 19355* (NCU); Robeson, *Britt 2506* (WIS); Sampson, *Campbell 4000* (GH); Scotland, *Godfrey 6964* (GH); Transylvania, *Freeman 56938* (NCU); Tyrrell, *Radford 42535* (NCU); Wake, *Ashe s.n., s.d.* (NCU); Warren, *Ahles & Bell 21837* (NCU); Washington, *Radford 42352* (NCU); Wayne, *Burk s.n.,* 1958 (NCU); Yancey, *Freeman 58353* (NCU). SOUTH CAROLINA: Aiken, *Ravenel s.n., s.d.* (NY); Anderson, *Davis 7919* (MO); Barnwell, *Batson & Kelley s.n.,* 1952 (NCU); Berkeley, *Ahles 35461* (NCU); Clarendon, *Campbell 4005* (GH); Dorchester, *Ahles & Haesloop 37783* (NCU); Hampton, *Bell 5351* (NCU); Lexington, *Radford 29889* (FSU, NCU); Pickens, *Rodgers 246* (DUKE); Sumter, *Holdaway 46* (DUKE). GEORGIA: Bartow, *Duncan 13268* (GA, GH); Emanuel, *Plummer & Pullen s.n.,* 1962 (NCU); Forsyth, *Duncan 9028* (GA); Irwin, *Harper 1709* (GH, MO, NY); Rabun, *Duncan 1047* (GA); Thomas, *Campbell 3921* (GH); Toombs, *Hardin & Duncan 14585* (NCU); Ware, *Campbell 4142* (GH). FLORIDA: Alachua, *Godfrey & Morrill 52620* (FSU); Bay, *Godfrey 61628* (FSU, VDB); Brevard, *Fredholm 6197* (GH, US); Columbia, *Ashe s.n.,* 1929 (NCU); Duval, *A. H. Curtiss 3639c* (FLAS, GH, NCU, US, W); Escambia, *Campbell 3950* (GH); Gulf, *Chapman s.n.,* 1893 (NY); Jackson, *Campbell 3915* (GH); Jefferson, *Godfrey 75826* (FSU); Lake, *Campbell 4109* (GH); Leon, *Kral 1801* (FSU, GH); Liberty, *Campbell 4073* (GH); Orange, *Meislahn 53* (US); Polk, *Jennings s.n.,* 1931 (USF); Putnam, *Godfrey 76895* (FSU); Santa Rosa, *Godfrey 76192* (FSU); Wakulla, *Godfrey 72248* (FSU). KENTUCKY: Casey, *Braun 2680* (US); Laurel, *Braun s.n.,* 1933 (US); McCreary, *Rogers 37* (GA, GH, MICH, MO, NY); Montgomery, *Wharton 5375* (GH, MICH, NY); Rowan, *Braun 2085* (US). TENNESSEE: Bledsoe, *Shanks et al. 3555* (NCU, TENN); Blount, *Sharp et al. 32416* (TENN, VDB); Coffee, *DeSelm et al. s.n.,* 1963 (NCU); Cumberland, *Shanks & Norris 7304* (TENN, US); Fentress, *Shanks 3076* (TENN, VDB); Grundy, *Kral 44545* (VDB); Morgan, *Shanks 3062* (TENN); Polk, *Clebsch 20217* (NCU, TENN). ALABAMA: Baldwin, *Campbell 3805* (GH); Cullman, *Eggert s.n.,* 1897 (MO, NY, US); Jackson, *Chase 4488* (US); Lee, *Earle & Baker s.n.,* 1897 (MO); Mobile, *Sargent s.n.,* 1941 (US); Pike, *Leland s.n., s.d.* (GH). MISSISSIPPI: Forrest, *Rogers 4735* (MISS); Greene, *Rogers 2509* (TENN); Harrison, *Tracy 4699* (MICH, NCU, NY, TAES, W); Jackson, *Tracy 3802* (MICH, MO); Lamar, *Sargent 144* (GH); Pearl River, *Amacker s.n.,* 1938 (MISSA); Tishomingo, *Anonymous s.n.,* 1937 (MISSA). ARKANSAS: Pulaski, *Engelmann 80* (MO); Saline, *Moore 321117* (WIS).

Andropogon glomeratus var. *glomeratus* is not as aggressive a colonizer as its two hypothetical derivatives, *A. glomeratus* vars. *hirsutior* and *glaucopsis.* Plants in the northern part of the range of var. *glomeratus* tend to be of shorter stature and to have shorter peduncles.

Andropogon glomeratus var. *glomeratus* and the robust variant of var. *pumilus* have inflorescences so similar in shape that most previous workers have united them and have overlooked the differences between them. The robust variant is taller, usually with rather smooth sheaths and with shorter, more ciliate, and darker ligules, narrower raceme sheaths, and lower glume keels that are scabrous below the middle. Although both taxa grow in wet sites, the robust variant is weedier, shows a greater tolerance for drier conditions and various soil types, and has a wider geographic range.

9b. **Andropogon glomeratus** (Walter) B.S.P. var. **hirsutior** (Hackel) Mohr, Bull. Torrey Bot. Club **24:** 21. 1897. Based on *Andropogon macrourus* Michaux var. *hirsutior* Hackel in DC. Monogr. Phanerog. **6:** 409. 1889. TYPE: Alabama, Mobile County, *Mohr s.n.,* 1884 (holotype, W!). *Andropogon virginicus* L. var. *hirsutior* (Hackel) Hitchc. Jour. Wash. Acad.

Sci. **23:** 456. 1933. *Andropogon virginicus* L. var. *tenuispatheus* (Nash) Fern. & Griscom f. *hirsutior* (Hackel) Fern. & Griscom, Rhodora **37:** 142. 1935. FIGURES 11, Q; 50.

DIAGNOSIS. Inflorescences (linear)-oblong; peduncles and usually spikelets short; stamens usually marcescent within spikelet.

DISTRIBUTION. Ditches, swales, bogs, flatwoods, and savannas, often forming very large populations in cleared, low ground. Coastal Plain from Maryland to Mississippi (MAP 18).

REPRESENTATIVE SPECIMENS. **United States.** MARYLAND: Somerset, *Hermann 9973* (GH, NY). VIRGINIA: Greensville, *Kral 14297* (USF); Isle of Wight, *Fernald & Long 6760* (GH, NY); Nansemond, *Fernald & Long 10944* (US); Northampton, *Fernald et al. 5181* (GH, NY, USF); Southampton, *Campbell 4216* (GH); Sussex, *Fernald & Long 7308* (GH). NORTH CAROLINA: Bertie, *Godfrey 7006* (GH); Bladen, *Ashe s.n., s.d.* (NCU); Brunswick, *Bell 16247* (NCU); Chowan, *Ahles & Duke 51035* (USF); Craven, *Godfrey & White 6768* (GH); Cumberland, *Ahles 36560* (NCU); Duplin, *Ahles 35747* (GH, NCU); Greene, *Radford 40434* (NCU, VDB); Halifax, *Ahles & Leisner 20845* (FSU, NCU, USF); Hertford, *Ahles & Haesloop 52210* (NCU); Hoke, *Correll 7181* (UC); Hyde, *Fosberg 17744* (MICH); Johnston, *Radford 29144* (NCU, USF); Lenoir, *Radford 31591* (NCU); Nash, *Godfrey & Kerr 6623* (GH, MO); Pitt, *Radford 41741* (NCU); Richmond, *Radford 19335* (NCU); Robeson, *Ahles 37253* (NCU); Sampson, *Campbell 3996* (GH); Tyrrell, *Radford 42553* (NCU); Wayne, *Burk s.n.,* 1958 (NCU); Wilson, *Radford 40781* (NCU). SOUTH CAROLINA: Bamberg, *Ahles 37658* (NCU); Chesterfield, *Radford 18679* (NCU); Clarendon, *Radford 30899* (NCU); Darlington, *Coker s.n.,* 1909 (NCU); Jasper, *Campbell 3964* (GH). GEORGIA: Berrien, *Celarier s.n.,* 1953 (MO); Brantley, *Campbell 4024* (GH); Colquitt, *Godfrey 76081* (FSU); Grady, *Komarek s.n.,* 1977 (FSU); Terrell, *Duncan 1772* (GA); Thomas, *Campbell et al. 4058* (GH); Ware, *Campbell 4141* (GH). FLORIDA: Alachua, *Chase 4216* (MICH); Baker, *Campbell 3851* (GH); Clay, *Campbell 4199* (GH); Duval, *A. H. Curtiss 3639b* (GA, MISSA, MO); Hillsboro, *Combs 1358* (US); Jackson, *Campbell 3810* (GH); Jefferson, *Godfrey 75830* (FSU); Lake, *Campbell 4131* (GH); Liberty, *Campbell 4074* (GH); Leon, *Silveus 6710-B* (GA, TAES); Madison, *Godfrey 75833* (FSU); Martin, *Campbell 3875* (GH); Orange, *Combs & Baker 1134* (NY); Polk, *Jennings s.n.,* 1923 (USF); Santa Rosa, *Godfrey 76803* (FSU); Seminole, *Hood s.n.,* 1911 (MO); Wakulla, *Godfrey 76239* (FSU); Walton, *Godfrey 75762* (FSU). ALABAMA: Baldwin, *Campbell 3804* (GH); Mobile, *Mohr s.n.,* 1896 (NCU); Washington, *Kral 49069* (VDB). MISSISSIPPI: Harrison, *Tracy 4699* (MO).

Earlier workers failed to appreciate the great similarity of *Andropogon glomeratus* vars. *hirsutior* and *glaucopsis* probably because they overlooked the numerous similarities in overall size, inflorescence appearance, and ligule morphology, as well as in morphological characters associated with the predominantly cleistogamous flowering mode. The varieties are also remarkably alike in geographic distribution and ecological preferences. They colonize extensively, much more so than their closest relative, *A. glomeratus* var. *glomeratus,* and form very dense populations in the moist, cleared ground of recently harvested timberlands. Often the two grow together in populations of thousands of individuals.

Because they grow together so frequently and are morphologically so alike, the possibility that they are not distinct taxa but merely genetic segregates of one another has been carefully considered. Based on observations of several hundred seedlings grown from seeds from both taxa (growing together in nature), there is no evidence for genetic segregation. The glaucousness/greenness and pubescence/glabrousness of the stem sheaths are discernible in the seedlings within a few weeks of germination. (Stem-sheath scabrousness often does not develop in the greenhouse in var. *hirsutior.*) The seedlings consistently match their parents in these two characters.

These taxa are unusual in the virginicus complex because their morphological differences are not associated with differences in either ecology or geography. The two taxa are recognized as varieties within the virginicus complex because they are more easily distinguished from one another than are the variants.

Andropogon glomeratus var. *hirsutior* resembles three other taxa besides *A. glomeratus* vars. *glomeratus* and *glaucopsis.* It has long been confused with individuals of the robust variant of *A. glomeratus* var. *pumilus* with a narrow inflorescence. The two can be distinguished by sheath scabrousness, ligule morphology, raceme-sheath width, peduncle length, and lower-glume-keel scabrousness. *Andropogon glomeratus* var. *hirsutior* is narrower in both ecological preference and geographic range than the robust variant. A closer morphological similarity exists between var. *hirsutior* of the southeastern United States and the southwestern variant of var. *pumilus.* Indeed, the differences (ligule margin, lower-glume scabrousness, and sometimes inflorescense denseness) are small and are not always easily discerned. Finally, in general aspect, var. *hirsutior* and the deceptive variant of *A. virginicus* var. *virginicus* are very close. They are separated by stem-sheath scabrousness and ligule morphology.

9c. **Andropogon glomeratus** (Walter) B.S.P. var. **glaucopsis** Mohr, Bull. Torrey Bot. Club **24:** 21. 1897. Based on *Andropogon macrourus* Michaux var. *glaucopsis* Ell. Bot. S. Carolina Georgia **1:** 149, 150. 1816. TYPE: South Carolina, *Elliott 181* (holotype, CHARL, not seen; isotype,[11] PH!). *Andropogon glaucopsis* (Ell.) Nash in Small, Fl. SE. U. S. 63. 1903. *Andropogon virginicus* L. var. *glaucopsis* (Ell.) Hitchc. Am. Jour. Bot. **21:** 139. 1934. FIGURES 11, R; 54; 55.

Andropogon glaucus Muhl. Descr. uber. Gramin. 278. 1817. Not *Andropogon glaucus* Retz., 1789. TYPE: South Carolina, *Elliott 181* (holotype, CHARL, not seen; isotype, PH!). *Cymbopogon glaucus* (Muhl.) Schultes, Mant. Syst. Veg. **2:** 459. 1824.

DIAGNOSIS. Stem sheaths smooth; leaves glabrous, glaucous; racemes short.

DISTRIBUTION. Flatwoods, bogs, ditches, swamps, pond margins, and swales. Coastal Plain from southern Virginia to Mississippi (MAP 19).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA: Princess Anne, *Fernald & Griscom 2765* (GH, USF). NORTH CAROLINA: Bertie, *Campbell 3991* (GH); Bladen, *Ahles 37350* (NCU); Carteret, *Phipps et al. 3688* (NCU); Craven, *Ahles & Duke 51035* (NCU); Dare, *Blomquist 8081* (GH); Greene, *Radford 40373* (NCU, UC); Jones, *Radford 39837* (NCU); New Hanover, *Canby s.n.*, 1867 (NY); Onslow, *Moldenke 122* (NY); Pamlico, *Godfrey & White 6813* (GH); Pender, *Ahles 36208* (NCU); Sampson, *Campbell 3995* (GH); Wake, *Ashe s.n., s.d.* (MO); Wayne, *Radford 31503* (NCU). SOUTH CAROLINA: Chesterfield, *Radford 18679* (NCU); Dorchester, *Ahles & Haesloop 37784* (NCU); Georgetown, *Radford*

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[11] Smith (1962) equated the Elliott specimen at PH to the specimen with the same number at CHARL.

31379 (GA, NCU); Horry, *Duke 0064* (NCU); Jasper, *Campbell 3963* (GH). GEORGIA: Brantley, *Campbell 4023* (GH); Camden, *Duncan & Hardin 14390* (NCU); Charlton, *Harper 693* (NY); Chatham, *Mellinger s.n.*, 1958 (GH); Lowndes, *Quarterman 5345* (VDB); McIntosh, *Duncan 20673* (GH, MICH, NCU, USF, WIS); Thomas, *Campbell 4229* (GH); Tift, *Shepard 220* (TAES); Ware, *Silveus 5368* (TAES); Wayne, *Campbell 4205* (GH). FLORIDA: Alachua, *Godfrey & Morrill 52618* (FSU); Baker, *Godfrey 74664* (FSU, NCU, VDB); Bay, *Godfrey 76141* (FSU); Brevard, *Shuey & Poppleton 1540* (USF); Clay, *Campbell 4200* (GH); Columbia, *Combs & Rolf 128* (US); Dixie, *Godfrey 56176* (FSU, GA, NY, USF); Duval, *A. H. Curtiss 6077* (GA, GH, MO, NY); Franklin, *Godfrey 71208* (FSU); Highlands, *Brass 14612* (GH); Indian River, *Tracy 9255* (TAES); Jackson, *Campbell 3812* (GH); Jefferson, *Godfrey 74599* (FSU, NCU, VDB); Lafayette, *Godfrey 74631* (FSU, NCU); Lake, *Campbell 4132* (GH); Leon, *Campbell & Godfrey 4062* (GH); Liberty, *Campbell 4072* (GH); Madison, *Kral 3760* (FSU, GH, NCU); Manatee, *Tracy 7735* (GH, MO, NY, TAES, W, WIS); Martin, *Campbell 4128* (GH); Orange, *Campbell 3908* (GH); Osceola, *Ray et al. 10493* (USF); Pasco, *Ray 9605* (GH, NCU, USF); Polk, *McFarlin 3747* (MICH); Putnam, *Silveus 6743* (LA, TAES); Santa Rosa, *Godfrey 76798* (FSU); Taylor, *Kral 52127* (VDB); Volusia, *Hood s.n.*, 1911 (GA); Wakulla, *Godfrey 64977* (FSU, VDB). ALABAMA: Baldwin, *Campbell 3806* (GH); Mobile, *Iltis et al. 21367* (WIS). MISSISSIPPI: Harrison, *Demaree 36240* (FSU, MISSA, TAES, VDB); Jackson, *Caldwell 368* (FSU).

Andropogon glomeratus var. *glaucopsis* and both the drylands and wetlands variants of *A. virginicus* var. *glaucus* have been combined by some authors (Nash, 1912) and confused by many botanists. *Andropogon glomeratus* var. *glaucopsis* differs from *A. virginicus* var. *glaucus* in its longer ligules and leaves and can be distinguished from the drylands variant by its pubescence below the raceme sheath, its inflorescence shape, and its habitat. Although these three differences do not hold for var. *glaucopsis* and the wetlands variant, the former has shorter raceme sheaths and racemes than the latter.

9d. **Andropogon glomeratus** (Walter) B.S.P. var. **pumilus** Vasey, Bot. Gaz. **16:** 27. 1891. TYPE: Texas, Val Verde County, *Neally 256,* 1890 (holotype, US, not seen; isotype, UC!, W!).

Andropogon glomeratus (Walter) B.S.P. var. *tenuispatheus* Nash in Small, Fl. SE. U.S. 61. 1903. TYPE:[12] Florida, Duval County, *A. H. Curtiss 5337,* 1894 (lectotype, NY!; isolectotypes, GA (two sheets)!, GH!, NY!, W!). *Andropogon tenuispatheus* (Nash) Nash, N. Am. Fl. **17:** 113. 1912. *Andropogon virginicus* L. var. *tenuispatheus* (Nash) Fern. & Griscom, Rhodora **37:** 142. 1935. *Andropogon virginicus* L. var. *hirsutior* (Hackel) Hitchc. f. *tenuispatheus* (Nash) Fern. & Griscom, Rhodora **42:** 416. 1940. *Anatherum virginicum* (L.) Sprengel subvar. *tenuispatheum* (Nash) G. Roberty, Boissiera **9:** 213. 1960.

DIAGNOSIS. Keels of lower glumes often scabrous to below middle.

DISTRIBUTION. Moist, disturbed sites (e.g., roadsides, fresh or brackish swamps, swales, moist woods, and fields). Virginia to California and south; extremely common through Mexico and Central America to northern South America; common throughout West Indies (MAP 20).

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[12] One of the many specimens annotated by Nash and at NY has been selected as the lectotype.

MAP 20. Distribution of *Andropogon glomeratus* var. *pumilus* (dots, robust variant; stars, southwestern variant).

9d. 1. **Robust variant** FIGURES 11, P; 51.

DIAGNOSIS. Stem sheaths usually smooth; ligules usually short; raceme sheaths narrow.

DISTRIBUTION. See distribution under variety for ecological preferences of this variant. One of most aggressive and ubiquitous weeds in North America. Throughout distribution of variety except southwestern United States and northwestern Mexico (MAP 20).

REPRESENTATIVE SPECIMENS. **United States.** VIRGINIA: Isle of Wight, *Fernald & Long 13887* (GH, MO, NY); Middlesex, *Hermann & Martin s.n.,* 1939 (MICH, NY, TENN); Nansemond, *Fernald et al. 15197* (GH, NY); Norfolk, *Fernald & Griscom 2766* (GH, USF). NORTH CAROLINA: Beaufort, *Blomquist 8027* (DUKE, NY); Brunswick, *Blomquist & Correll 4866* (DUKE, GA); Camden, *Campbell 3984* (GH); Carteret, *Blomquist 10201* (FSU, GH); Hyde, *Radford 42624* (NCU, VDB); Robeson, *Ahles 37323* (NCU); Scotland, *Sharp 2008* (NCU). SOUTH CAROLINA: Abbeville, *Radford 30739* (NCU); Beaufort, *Bell 5264* (NCU); Calhoun, *Ahles 35328* (NCU); Charleston, *Duncan 5775* (GA); Chester, *Bell 10050* (NCU); Jasper, *Campbell 3965* (GH); Kershaw, *Radford 29957* (NCU); Laurens, *Bell 10105* (NCU); McCormick, *Radford 30717* (GH, NCU); Spartanburg, *Bell 10372* (NCU). GEORGIA: Berrien, *Celarier A-2600-1* (MO, UC); Clarke, *Duncan 286* (GA); Clinch, *Faircloth & Cribbs 5003* (GA, MO, NCU); Harris, *Jones 22345* (GA, GH); McIntosh, *Duncan 20634* (GH, NCU, USF, WIS); Pike, *Duncan 3064* (GA, MICH, USF); Putnam, *Cronquist 4759* (GA, GH, MO, NY); Thomas, *Campbell et al. 4055* (GH); Sumter, *Harper 651* (NY); Washington, *Duncan 4342* (GA, MISS). FLORIDA: Alachua, *D'Arcy 2166* (GA, VDB, WIS); Baker, *Campbell 3850* (GH); Broward, *Stimson 852* (FSU, NCU, USF); Citrus, *Godfrey 65108* (FSU); Collier, *Lakela 27803* (GA, USF); Dade, *Gill s.n.,* 1970 (GH, MO, USF); Duval, *A. H. Curtiss 6078* (GA, GH, MO, NCU, NY); Escambia, *Hansen 2349* (FSU, WIS); Franklin, *Godfrey 71124* (FSU); Highlands, *Campbell 4117* (GH); Hillsboro, *Perdue 1748* (FSU, GH, NCU, TAES, UC, USF); Jackson, *Campbell 4030* (GH); Leon, *Wooten 2320* (FSU, VDB); Liberty, *Godfrey 55529* (FSU); Madison, *Godfrey 74115* (FSU, NCU, VDB); Manatee, *Perdue 1788* (FSU, GH, NCU, TAES, UC); Monroe, *Campbell 3730* (GH); Nassau, *Godfrey 74691* (FSU, VDB); Osceola, *Fredholm 6106* (GH, MO, US); Palm Beach, *Kral 5690* (FSU, VDB); Pinellas, *Deam 2767* (MO, NY); Santa Rosa, *Meriläinen & Roe 912* (NCU, WIS); St. Johns, *Ward 2305* (FSU, GH, NCU, USF, VDB); Taylor, *Godfrey 74145* (FSU, NCU, VDB). Alabama: Baldwin, *Campbell 3801* (GH); Barbour, *Campbell 4152* (GH); Lee, *Jones s.n.,* 1959 (GA, NCU); Marshall, *Golden s.n.,* 1974 (VDB); Mobile, *Tracy s.n.,* 1896 (MISSA); Montgomery, *Campbell 3958* (GH); Sumter, *Jones 1730* (NCU). Mississippi: Bolivar, *Temple 4669* (MISS, NCU); Clarke, *Jones 10711* (MISS); Hancock, *Demaree 36318* (FSU, GA, GH, MISSA, NCU, TAES, VDB); Harrison, *Demaree 34532* (NCU, USF, VDB); Jackson, *Demaree 34429* (FSU, NCU, TAES, USF, VDB); Jasper, *Jones 10851* (MISS); Jefferson, *McDougall 1171* (US); Lauderdale, *Campbell 3954* (GH); Oktibbeha, *Tracy s.n.,* 1890 (MISSA, NY, TAES); Warren, *Colvin s.n.,* 1938 (MISSA); Wayne, *Campbell 3952* (GH). Arkansas: Ashley, *Demaree 18562* (GH, MO, NY, WIS); Bradley, *Demaree 21820* (GA, MO, NY); Desha, *Demaree 21627* (NY, TENN, UC, WIS); Garland, *Demaree 46698* (TAES); Howard, *Demaree 45229* (TAES); Phillips, *Palmer 26645* (GH, MO); Pike, *Demaree 9979* (GH, MO, NY, UC, USF); Saint Francis, *Demaree 59675* (TENN, VDB). Louisiana: Bienville, *Sharpe 480* (USF); Caddo, *Thomas & Overby 32838* (NCU); Concordia, *Thomas & DePoe 510* (NCU, TENN); East Baton Rouge, *McCoy s.n.,* 1952 (NY); Iberia, *Delahoussaye 158* (VDB); Jackson, *Kral 16073* (FSU, VDB); Natchitoches, *Palmer 8865* (MO, NY); Orleans, *Ewan 18792* (GH, MO); West Carroll, *Demaree 14096* (GH, MO, NY); Vermilion, *Reese 3906* (FSU, GH, NCU). Oklahoma: Cleveland, *Goodman 2362* (GH, MO, NY); Johnston, *Waterfall 5685* (MO, NY); Marshall, *Goodman 7389* (UC, WIS); *McLain, Massey, & Hoisington 1491* (NCU); Murray, *Hopkins 1121* (MO); Payne, *Gay 130* (USF); Pontotoc, *Robbins 3202* (NY, TAES, UC). Texas: Anderson, *Gould 7285* (TAES); Austin, *Parks & Cory 17704* (GH, TAES); Fort Bend, *Anderwald s.n.,* 1949 (TAES); Brazos, *Beason 8* (TAES); Caldwell, *Plank 2* (TAES); Camp, *Turner 13-F* (TAES); Dallas, *Reverchon 3440* (GH, MO, NY); DeWitt, *Riedel s.n.,* 1941 (MO); Fayette, *Plank s.n.,* 1893 (NY); Freestone, *Kral 82* (FSU); Galveston, *Waller & Bauml 3159* (GH, TAES); Gonzales, *Tharp & Barkley 13006* (GH, NY, UC, VDB); Gregg, *York s.n.,* 1941 (GH, NY); Hidalgo, *Clover 462* (MICH); Karnes, *Johnson 1107* (TAES); Kerr, *Cory 52397* (GH, MICH, NY, UC); Motley, *Parks & Cory 15964* (GH, TAES); Real, *Cory 24353* (GH); Tarrant, *Whitehouse 17320* (MICH, NY); Tom Green, *Cory 5103* (GH); Uvalde, *Parks & Cory 7501* (TAES); Walker, *Cory 50637* (MICH, NY); Wharton, *Palmer 6629* (MICH, MO). **Mexico.** Chihuahua: Río Bonito, *LeSueur 0100* (CAS, GH, TEX, UC). Coahuila: Las Delicias, *Stewart 2818* (GH). Nuevo León: Cola de Caballo, *Beetle M-414* (FLAS); Monterrey, *Smith M593* (TEX). Tamaulipas: El Limón, *Kenoyer & Crum 3611* (GH, MICH); Gd. Wanteon, *Harvey & Witherspoon 9214* (MICH); Jaumave, *Stanford et al. 2359* (CAS, GH). Durango: Coyotes, *Maysilles 8294* (MICH, TEX, UC); Durango, *Palmer 251* (F, GH, MICH, UC). San Luis Potosí: Tamazunchale, *Edwards 944* (TEX), *Fisher 37133* (GH), *Kenoyer A597* (F, MICH). Jalisco: Guadalajara, *Palmer 466* (GH, UC, W); Villa Corona, *McVaugh 14415* (MICH). Michoacán: Volcán Parícutin, *Hakala s.n.,* 1946 (MICH). Hidalgo: Jacala, *Kral 24887* (VDB). México: Ixtapan de la Sal, *Harvey 8661* (MICH). Puebla: Cotimehuaca, *Arsène 3542* (GH); El Carrizal, *Pineda s.n.,* 1968 (CAS, MICH), *Arsène 1433* (GH), *Nicolas s.n.,* 1909 (GH). Veracruz: Cordoba, *Matuda 330* (MICH, VT), *Bourgeau 1666* (GH), *Cyasto 330* (VT); Jalapa, *Gould 9261* (MICH, TEX); Nautla, *Beetle M-1265* (WIS); Papantla, *Gutierrez s.n.,* 1967 (CAS, MICH); Orizaba, *Seaton 111* (F, GH), *Müller 2033* (W); San Salvador de Acajete, *Sharp 45622* (GH). Oaxaca: San Antonio, *Smith 960* (F), *Pringle 5565* (GH, VT). Chiapas: Chanal, *Kaplan 126ch57* (F); Ixtapa, *Laughlin 1076* (CAS); La Trinitaria, *Breedlove 41938* (CAS); Ocozocoantla de Espinosa, *Breedlove 37797* (CAS); Pueblo Nuevo Solistahuacan, *Lathrop 5215* (CAS), *Breedlove 19931* (CAS); Rayon, *Breedlove 10159* (CAS, F); San Cristobal, *Breedlove 11915* (F, MICH); Tenejapa, *Breedlove 10926* (MICH, TEX), *Ton 1041* (F, MICH); Teopisca, *Breedlove 10545* (CAS, TEX); Venustiano Carranza, *Laughlin 1989* (CAS); Yerba Buena, *Mill 572* (CAS); Zinacantan, *Laughlin 2258* (CAS). CAMPECHE: Bolonchen de Rejon, *Gould 12626* (UC); Carmen, *Kral 25422* (MICH, VDB), *Rzedowski 26384* (CAS, F, MICH, TEX). YUCATÁN: Progreso, *Swallen 2911* (MICH); Sisal, *Gould 12641* (UC); Tizimín, *Gould 12652* (UC). QUINTANA ROO: Lake Chichancanab, *Swallen 2729* (MICH); Coba, *Lundell 7835* (MICH); Payo Obispo, *Dampf s.n.*, 1925 (F). **Belize:** Buttonwood Cay, *Fosberg & Spellman 54411* (F); Corozal, *Lundell 4902* (CAS, GH, MICH, TEX), *Gentle 134* (MICH); Honey Camp, *Lundell 428* (F, GH, US); Southwest Cay Is., *Fosberg & Stoddard 53860* (US); Tower Hill Estate, *Karling 55* (F). **Guatemala.** ALTA VERAPAZ: Cobán, *Molina s.n.*, 1963 (F); Tamahu, *Standley 70928* (F). ESCUINTLA: between Escuintla and Santa Lucía Cotz[umalguapa], *Standley 63414* (F). HUEHUETENANGO: Cuilco, *Steyermark 50800* (F, US); Ixcan, *Steyermark 49337a* (F). IZABAL: Cristina, *Blake 7570* (US), *Steyermark 38479* (F). EL PETÉN: La Libertad, *Lundell 3482* (GH, MICH, US); Tikal, *Contreras 86* (F, TEX). SACATEPÉQUEZ: Antigua, *Standley 64695* (F). SOLOLÁ: Volcán Atitlán, *Steyermark 47475* (F); Volcán San Pedro, *Steyermark 47187* (F). **El Salvador:** Matapán, *Boden s.n.*, 1900 (MO). **Nicaragua:** Managua, *Garnier 818* (MICH); Puerto Cabezas, *Pederson s.n.*, 1968 (WIS). **Costa Rica:** Cartago, *Weston et al. 3471* (UC); Puntarenas, *Pohl & Davidse 10794* (UC); San José, *Hitchcock 8465* (MICH), *Pohl & Davidse 11433* (UC). **Panama:** Barro Colorado Is., *Woodworth & Vestal 542* (F, GH); Canal Zone, *Hitchcock 8033* (US), *Standley 31228* (US); Chiriquí, *McCorkle C-53* (FSU). **Bermuda:** *Manuel 776* (GH). **Bahama Islands:** Andros, *Northrup 659* (GH); Cat Is., *Byrne 297* (GH, WIS); Grand Bahama, *Correll 40635* (TEX), *Correll & Kral 42899* (VDB); Great Inagua, *Dunbar 234* (GH); South Bimini, *Howard 10208* (GH). **Turks and Caicos Islands:** Caicos Is., *Correll 43117* (GH). **Greater Antilles.** CUBA. Habana: Cajio, *León 14697* (GH); Santiago de las Vegas, *Wilson 2207* (MICH, W). Las Villas: Manajanabo, *León 5302* (GH); Sancti-Spiritus, *León 3024* (GH); Soledad, *Howard 6230* (GH, US). Isla de Pinos: Nueva Gerona, *A. H. Curtiss 294* (GH), *Killip 44531* (US). Camagüey: Cayo Romano, *Shafer 2614* (GH). Oriente: Moa, *Bristol 191* (GH); Monte Verde, *Wright 1555* (GH); Sierra de Nipe, *Ekman 6376* (MICH). JAMAICA: Manchester, *Webster & Proctor 5252* (GH, MICH); Port Antonio, *Maxon & Killip 288* (US); St. Thomas, *Crosby et al. 825* (GH, TEX, UC). HAITI: Île de la Tortue, *Ekman 4263* (GH, US); Morne des Commissaires, *Holdridge 1324* (MICH, TEX); Port au Prince, *Beech 2048* (US), *Potter 5008* (GH); Sur Cayer, *Ekman 72* (US). DOMINICAN REPUBLIC: Barahona, *Howard 8584* (GH), *Fuentes 1281* (GH); Leybo Province, Puenta Icacos, *Ekman 15787* (GH, TEX). PUERTO RICO: Isla Verde, *Blomquist 11758* (UC). GRAND CAYMAN: *Brunt 1656* (FLAS, NCU). **Lesser Antilles.** ST. KITTS: *Hitchcock 16361* (US). ANTIGUA: *Box 128* (US). GUADELOUPE: *Questel 1422* (US), *Duss 3548* (US). MARTINIQUE: *Duss 1301* (US). **Colombia:** San Andros Is., *Gentry s.n.*, 1967 (WIS). **Venezuela.** FALCÓN: *Wingfield 5417* (MO).

The robust variant is a remarkably aggressive colonizer in a wide variety of soils. It does not characteristically invade old fields and cleared timberlands with the regularity of *Andropogon virginicus* or other taxa of *A. glomeratus*. Instead, it prefers some flow of water in the soil and often chokes roadside ditches with its dense growth (FIGURE 27).

In the greenhouse and the experimental garden it has consistently been the fastest-growing member of the virginicus complex. In the field it produces the thickest stems and the largest leaves. It appears to have some adaptations for very rapid growth, but at the same time it is phenotypically plastic in plant height. Under poorer conditions its stems may be very short, although the inflorescence remains densely and profusely branched.

The robust variant tolerates a greater range of soil salinity and pH than do other members of the virginicus complex. It grows in either brackish or fresh water and in soils derived from either acidic or alkaline rocks.

The uniquely wide ecological preferences and geographic range and the distinctive morphology of this variant argue for species ranking. On the other hand, certain individuals are very similar in general appearance to *Andropogon glomeratus* vars. *glomeratus* and *hirsutior.* The ways in which the variant differs from these two varieties have been discussed under the varieties. Furthermore, the next taxon forms a bridge between the robust variant and the rest of *A. glomeratus,* which makes the species large but coherent.

Small or shaded plants of the robust variant may resemble the deceptive variant of *Andropogon virginicus* var. *virginicus* in overall size and inflorescence shape. The two taxa differ in stem-sheath pubescence, peduncle length, and lower-glume-keel scabrousness.

9d. 2. **Southwestern variant** FIGURE 52.

DIAGNOSIS. Stem sheaths always scabrous; ligules long; spikelets often exceeding 4 mm in length.

DISTRIBUTION. Moist soils of seepage slopes and edges of springs. Utah to California, south to northwestern Mexico (MAP 20).

REPRESENTATIVE SPECIMENS. **United States.** NEW MEXICO: Grant, *Wright 2100* (GH, MO, NY, UC). ARIZONA: Santa Cruz, *Barr 63-504* (USF). NEVADA: no locality given, *Wheeler s.n.,* 1871 (GH). CALIFORNIA: Inyo, *Thorne & Tilforth 42512* (NY); Los Angeles, *Moxley 632* (MO, UC); Marin, *Howell s.n.,* 1939 (NY, UC); Placer, *Crampton 5802* (TAES); Riverside, *Reed 2901* (CAL, LA); San Bernardino, *Roos 5023* (NY, UC); Shasta, *Bacigalupi 2387* (GH); Ventura, *Pollard s.n.,* 1946 (MO, NY, UC); Yolo, *Beetle 4691* (TAES, UC, WIS). **Mexico.** BAJA CALIFORNIA NORTE: Cerro la Encantada, *Chambers 544* (CAS, UC); Santa María, *Moran 11492* (CAS, UC). BAJA CALIFORNIA SUR: Mission de San Pedro Martin Valley, *Wiggins 9036* (GH).

In the past this variant has been called *Andropogon glomeratus.* It is distinguished here for the first time as a morphologically and geographically isolated group of populations of *A. glomeratus* var. *pumilus.* Its chief taxonomic significance is that it shares some features (sheath scabrousness and ligule length) with the first two varieties of *A. glomeratus,* and others (peduncle length and scabrousness of the lower glumes) with the robust variant; it thus holds the species together. It appears to be closest to the robust variant because the two variants share the unique feature of scabrousness of the lower glume keels, a character generally more conspicuous in the southwestern variant. Their occurrence in the western United States and their preference for seepage conditions are further bases for combining them into one variety. Finally, while United States populations are fairly easily separated from the rest of var. *pumilus,* some populations in northern Mexico are more or less intermediate between the two variants. More collections and especially more field work in this area will be necessary to assess how these variants interact.

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APPENDIX A. **Glossary.**

CALLUS—the very base of the spikelet, covered with hairs in all members of the virginicus complex (FIGURES 1, 2, 8, and 9).

COLLAR—the region of the leaf at the junction of the blade and the sheath.

DISPERSAL UNIT—the spikelet and the attached rachis internode and pedicel (FIGURES 1, 2, 8, and 9).

INFLORESCENCE—the portion of the stem producing reproductive structures.

INFLORESCENCE UNIT—the racemes, the peduncle, and the subtending raceme sheath (FIGURE 11).

LIGULE—a membranaceous flange on the adaxial surface of the leaf at the collar (FIGURE 4).

PEDICEL—a short axis attached at its base to the rachis internode and with or without a vestigial spikelet (FIGURE 8).

PEDICELED SPIKELET—the spikelet at the apex of the pedicel; nonfunctional and reduced or absent in the virginicus complex (FIGURE 8).

PEDUNCLE—the axis subtended by the raceme sheath and bearing at its apex two or more racemes (FIGURE 11).

RACEME—the linear series of spikelets connected by the rachis internodes (FIGURE 11). "Rame," designating a structure with sessile and pediceled spikelets, has been used in *Andropogon* (Pohl, 1978).

RACHIS INTERNODE—the axis connecting the spikelets into racemes (FIGURE 8).

APPENDIX B. **Rules for determining distance between character states.***

I. For characters of type a ((low range) mean (high range); characters 1, 7, 8, 9, 29, and 31), type b (low range–high range; characters 10, 26, and 27), and type c ((low range) low mean–high mean (high range); characters 19, 20, 23, and 25), compare the ranges of types a and b and the intervals between the low and high means of type c, then assign a value based on the following conditions:
  0, if the range of each overlaps more than half the range of the other, or the range of one is totally contained within the range of the other.
  ½, if the range of one is less than or equal to half the range of the other.
  1, if the range of each overlaps that of the other by less than half.

II. For characters with two or three states (characters 2, 3, 5, 6, 11, 13, 18, 24, 28, 30, and 32):
  0, if identical for all states.
  ½, if different in one or more but not all states.
  1, if no states are shared.

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*See TABLES 4–6.

III. For the two pubescence characters (4 and 17):
   0, if identical in half or more of their states but different in less than two.
   ½, if identical in less than half of their states and different in two or or more.
   1, if no states are shared.

IV. For character 12:
   0, if identical in all states.
   ½, if identical in some states but different in others.
   1, if not identical in any states.

V. For character 14:
   0, if overlap is half the total range or more.
   ½, if overlap is less than half the total range, or if 1–2 vs. 2–3 or 2–3 vs. 3–4.
   1, if no overlap, or if 1–2 vs. 2–5 or 2–3 vs. 3–5.

VI. For character 15:
   0, if overlap is half the total range or more, or if the range of one lies entirely within the range of the other.
   ½, if overlap is less than half but more than 0 or if endpoints of two ranges are equal (e.g., 1–2 vs. 2–3, 2–4, 2–5, or 2–6; 2–3 vs. 3–5).
   1, if no overlap, or 2–3 vs. 3–7, 11.

VII. For character 16:
   0, if the mean of each falls within the range of the other.
   ½, if the mean of one lies outside the range of the other.
   1, if the mean of each lies outside the range of the other.

VIII. For character 22 there are three classes: A is 2 (3 or 4); B is 2–3, 2–4, or 2–5(–7); and C is 2–9 or 2–13. Distance is based on the following conditions:
   0, if classes are identical.
   ½, if class A vs. B.
   1, if class A or B vs. C.

IX. For character 21, there are three classes: A, if range of means is less than 10 (e.g., (2)4–6(12)); B, if range of means includes 10 (e.g., (1)6–14(60)); and C, if range of means is greater than 10 (e.g., (9)26–66(15)). Distance is based on the following conditions:
   0, if classes are identical.
   ½, if class A vs. B or B vs. C.
   1, if class A vs. C.

X. For character 33, there are three classes: A, mean less than 10%; B, mean 10–50%; and C, mean greater than 50%. Distance is based on the following conditions:
   0, if classes are identical.
   ½, if class A vs. B or B vs. C.
   1, if class A vs. C.

APPENDIX C. **Ambiguous names.**

Andropogon belvsii Desv. Opusc. Sci. Phys. Nat. 67. 1831. Type: no locality cited; this name based on an unnamed figure (*t. 23, fig. 4*) of Palisot de Beauvois, Essai Nouv. Agrost. 1812. Although Jackson (Index Kew. **1**: 124. 1893) equated this with *Andropogon argyreus* Schultes, and Hitchcock (1951) equated it with *Andropogon ternarius* Michaux, the illustration alone is not enough to determine the placement of this name.

Andropogon louisianae Steudel, Synopsis Pl. Glum. **1**: 383. 1854. The description ("spica solitaria") does not fit the *Andropogon virginicus* complex. Although Chase (1937) said the type of this name (p) is a "small, over-mature plant of *A. virginicus,*" in Hitchcock (1951) the name was doubtfully referred to *A. virginicus* L.

Andropogon virginicus L. subvar. *ditior* Hackel in DC. Monogr. Phanerog. **6**: 411. 1889. Types: Florida, Duval County, *A. H. Curtiss 3639d* (Curtiss distributed three species under this number: *Andropogon glomeratus* (Walter) B.S.P. var. *pumilus* Vasey, the robust variant (FLAS!, GA, MISSA!), *A. virginicus* L. var. *virginicus,* the deceptive variant (GH!), and *A. longiberbis* Hackel (GH!, NY (two sheets)!), none of which bears any indication that Hackel used them); Mexico, Veracruz, *Schiede 937* (not seen; Chase & Niles (1962) placed this collection in *Andropogon bourgaei* Hackel); and Mexico, *Liebmann 72* (not seen).

Hackel's description could apply to taxa of *Andropogon glomeratus, A. virginicus,* or *A. longiberbis.*

APPENDIX D. Synonymy of Andropogon ternarius Michaux.

Andropogon ternarius Michaux, Fl. Bor. Am. 57. 1803. TYPE: Carolina (holotype, P, not seen; photo, GH!).

a. *Andropogon ternarius* Michaux var. *ternarius*

Andropogon argenteus Ell. Bot. S. Carolina Georgia **1:** 148. 1816. TYPE: no locality given (CHARL, not seen, placed in this taxon by Scribner (1901)). *Sorghum argenteum* (Ell.) Kuntze, Rev. Gen. Pl. **2:** 790. 1891.

Andropogon argyreus Schultes, Mant. Syst. Veg. **2:** 450. 1824, *nomen superfl.* for *Andropogon argenteus* Ell. and with the same type. *Anatherum argyraeum* (Schultes) G. Roberty, Boissiera **9:** 209. 1960.

Andropogon muhlenbergianus Schultes, Mant. Syst. Veg. **2:** 455. 1824, *ex char.* TYPE: South Carolina, not seen.

Andropogon elliottii Chapman, Fl. So. U. S. 581. 1860. Based on *Andropogon argenteus* Ell., 1816. Not *Andropogon argenteus* DC., 1813. *Sorghum elliottii* (Chapman) Kuntze, Rev. Gen. Pl. **2:** 791. 1891.

Andropogon argyreus Schultes var. *tenuis* Vasey, Contr. U. S. Natl. Herb. **3:** 12. 1892, *ex char.* TYPE: Texas, not seen.

Andropogon argyreus Schultes var. *macra* Scribner, U. S. D. A. Div. Agrost. Bull. **1:** 20. 1895. TYPE: Florida, Duval County, *A. H. Curtiss 4592,* 1894 (holotype, not seen) (this name placed in synonymy of *Andropogon ternarius* Michaux by Hitchcock, 1951).

Andropogon elliottii Chapman var. *glaucescens* Scribner, Bull. Torrey Bot. Club **23:** 145. 1896. TYPE: Florida, Lake County, *Nash 473* (holotype, US, not seen; isotype, GH!). *Andropogon ternarius* Michaux var. *glaucescens* (Scribner) Fern. & Griscom, Rhodora **37:** 137, 138. 1935.

Andropogon scribnerianus Nash, Bull. New York Bot. Gard. **1:** 432. 1900. Based on *Andropogon elliottii* Chapman var. *glaucescens* Scribner. Not *Andropogon glaucescens* HBK., 1815.

Andropogon mississippiensis Scribner & Ball, U. S. D. A. Div. Agrost. Bull. **24:** 41. 1901, *ex char.* TYPE: Mississippi, Harrison County, *Tracy 3818* (holotype, not seen).

b. *Andropogon ternarius* Michaux var. *cabanisii* (Hackel) Fern. & Griscom, Rhodora **37:** 138. 1935. Based on *Andropogon cabanisii* Hackel, Flora **68:** 133. 1885. TYPE:* Florida, Gulf County, *Chapman s.n.,* 1884 (lectotype, W!). *Sorghum cabanisii* (Hackel) Kuntze, Rev. Gen. Pl. **2:** 791. 1891.

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
UNIVERSITY OF MAINE
ORONO, MAINE 04469

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*Hackel cited "Pennsylvania et Florida leg. Cabanis (in Herb. reg. Berolin.); Florida prope Appalachicola leg. Chapman." A specimen of the latter description from the Hackel herbarium is here selected as a lectotype.

THE PLATES OF AUBLET'S HISTOIRE DES PLANTES DE LA GUIANE FRANÇOISE

RICHARD A. HOWARD

IN THE COURSE of work on an unpublished manuscript of Alexander Anderson (a "hortus" of the botanical garden on St. Vincent, West Indies), reference to the drawings of Aublet's *Histoire des Plantes de la Guiane Françoise* was frequently necessary. Anderson, the second director of the botanical garden (1785–1811), collected in Trinidad and Tobago (1787, 1790) and the Guianas (1791). In describing the specimens or the plants later grown from seeds, he made frequent references to and comparisons with the work of Aublet. I have been unable to find any list of modern equivalents for the taxa in Aublet's work. The alphabetic list that follows was compiled from the existing literature in which Aublet names are mentioned or his specimens are cited.

In the second edition of *Taxonomic Literature* (1976), Stafleu and Cowan supplied several references to the life of Aublet and to the publication of his *Histoire des Plantes.* The commentaries of Lanjouw and Uittien (1940), Souilijaert and Stafleu (1953), Leandri (1968), and Bernardi (1976) are most useful. Froidevaux (1897), in a paper generally overlooked, has given Aublet's itinerary together with supporting documentation, both in considerable detail. Aublet's herbarium was purchased by Sir Joseph Banks, along with his drawings and notes. These are now all in the British Museum (Natural History); the notes and drawings have been bound separately and are housed in the library. Banks apparently shared the specimens with Linnaeus *filius,* whose collections are in the J. E. Smith herbarium at the Linnean Society. Additional collections are in several herbaria in Paris (Adanson, Jussieu, Rousseau) as well as at Stockholm, Copenhagen, and Vienna, with fewer specimens at Brussels, the Field Museum, Liverpool, Missouri, Uppsala, and possibly Geneva. In designating types, holotypes, or lectotypes most recent authors have cited specimens at the British Museum, although a few holotypes have been attributed to Paris, Vienna, and Geneva. Herbarium specimens have been sought (BM, LINN, P) as far as time permitted and are cited for each entry, either as supporting or typotype specimens or as designated in the literature or on annotation labels.

It is apparent from the articles studied that many of the drawings published by Aublet are mixtures, and in some cases the descriptions are composites of discordant elements. Many of Aublet's descriptions, therefore, have been emended by later authors, usually by the exclusion of the fruits or flowers. In a few cases, however, the illustration and description of the fruit represent the emended species description. Cuatrecasas, Johnston, Niedenzu, Sandwith, and

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others have rejected Aublet's names as *nomina dubia* or because the supporting specimens were mixtures. This procedure is no longer permissible under the International Code of Botanical Nomenclature. In many cases these names can be or have been typified by either excluding or accepting particular portions of specimens or the plate. In some instances designation of type material has resulted in new combinations being proposed in this paper—e.g., *Cordia tetraphylla* Aublet = *Buchenavia tetraphylla* (Aublet) Howard, replacing *Buchenavia capitata* (Vahl) Eichler. The suggestion that Aublet used native collectors and then described what was presented to him may well account for the mixture of materials. As will be indicated later, the error may also have occurred in the exchange between the artist and the engraver.

Stafleu (1971) noted that Aublet differed from many of the Linnaean school in his use of native names for the genera he proposed. He noted that other botanists almost immediately substituted more acceptable names for those proposed by Aublet, and that 27 of Aublet's names appear in the list of *nomina conservanda.* This can hardly be considered criticism of Aublet's work. Of the 576 genera in the publication, six of Aublet's proposed generic names are conserved: *Ouratea* unnecessarily, *Houmiri* and *Vochy* with orthographic changes, and only *Bacopa, Rourea,* and *Simarouba* on the basis of priority of publication. Of the 21 rejected names, one (*Cananga*) is a homonym; all the others apparently resulted from the proposer's preference for a better-known or more widely used name. The substitute names suggested by Scopoli (1777) and Schreber (1789, 1791) were adopted by a few then-contemporary authors. The specimens in the J. E. Smith herbarium, for example, bear the names used by Schreber. The equivalence of the Scopoli and Schreber names to those used by Aublet will be considered in a separate paper by Dr. James Zarucchi.

Stafleu and Cowan (1976) note that the publication of the *Histoire* was announced in March, 1775, and that copies were issued in June, 1775, but they suggest that publication extended over a period of time. In *Index Nominorum Genericorum Plantarum* (Farr *et al.,* 1979) the date of publication of June, 1775, is assumed. Gleason, Williams, and Henrey (see entries *Fothergilla* and *Tamonea*) have called attention to the fact that in some copies of the work the name *Tamonea* was used twice, while in others one entry was corrected to *Fothergilla,* clearly indicating that not all copies resulted from a single printing. Henrey (1975) has called attention to marks for the binders that indicate replacement pages.

Indexes to Latin and French names appear in volume two of the *Histoire* following the main body of the text and preceding the supplement in which additional species are described. Reference to the taxa described in the supplement appears in the index, however. The plates of the supplement, which are numbered 368–392, complete the second volume of plates.

In the list that follows there are many examples of Aublet's specific name for a taxon differing between the text, the index, and/or the plates. Most commonly, these involved the name of the country. Aublet was consistent in his spelling of "guianensis" in the text, and this has been adopted here as the correct spelling of that specific name. However, on the plates the same specific name has in most cases been spelled "guyannensis," and that spelling has been adopted in some modern floras or monographs. Other orthographic or typographic variations on "guyannensis" are reported.

The majority of the genera described by Aublet are monotypic. When several species were listed, Aublet gave a specific name in the text for all of them, except in the genera *Aeschynomene, Apocynum, Jussiaea, Myrtus, Periploca,* and *Tragia,* where species were often described in the text with supporting literature citations but without a specific epithet. For most of these unnamed taxa, a specific epithet is given in the index. Urban (1919, 1920) examined these and made the necessary additions of author or combination, as required. Thus, *Anechites nerium* (Aublet) Urban, *Eugenia pomifera* (Aublet) Urban, *Gonolobus scandens* (Aublet) Urban, *Myrcia citrifolia* (Aublet) Urban, and *Sesbania emerus* (Aublet) Urban have basionyms in which the specific epithet appears in the index in Aublet's work but not in the text. None of these taxa is illustrated. *Periploca umbellata* Aublet is antedated by *Echites corymbosa* Jacq. and is known today as *Forsteronia corymbosa* (Jacq.) Meyer. One name remains obscure: *Tragia scandens* Aublet (based on Plumier's Nova Pl. Gen. Amer. 14. 1703 and Pl. Amer. (Burmann, ed.), 250, *t. 252, fig. 1.* 1755) was not placed by Urban (Symb. Antill. **8**: 363. 1920).

A number of Aublet's taxa have not been satisfactorily placed. Among the new genera he described, the following do not have satisfactory modern placement: *Courimari* (Elaeocarpaceae?), *Macahanea* (Celastraceae?), *Managa* (Celastraceae?), *Meborea* (Euphorbiaceae?), *Senapea* (Passifloraceae?), *Singana* (Leguminosae?), and *Tontelea* (Celastraceae?).

Aublet's names for the monotypic genera *Aberemoa* (Annonaceae), *Evea* (Rubiaceae), and *Ropourea* (Flacourtiaceae) are *nomina rejicienda*—a designation that should be reconsidered on the basis of modern identifications of the taxa.

In compiling the following list of modern equivalents for the taxa illustrated in Aublet's plates, I have examined the comprehensive studies by Hallier (1918), Lanjouw and Uittien (1940), and Sandwith (1937, 1942, 1962, 1963). The many treatments in Pulle's *Flora of Suriname* (1932–1975) offered quick initial reference and were further checked in Lemée (1952–1956). More recent works of value in this search have been the several monographs in the *Flora Neotropica* series, as well as treatments by Maguire and collaborators in the "Botany of the Guayana Highland" series in the *Memoirs of the New York Botanical Garden* (1953–1978)—especially Steyermark's study of the Rubiaceae (Maguire, 1972), which differs so drastically from Bremekamp's earlier work in Pulle's *Flora of Suriname.* Other monographs and special papers are referred to in the text.

The following alphabetic listing of species in Aublet's *Histoire* provides reference to their description in the text (volumes 1 and 2, or the supplement) and their illustration in the plates. When the spelling of the specific name in the index or on the plate is different from that in the text, the variant spelling is given in parentheses. "NG" indicates that a new genus is described, and "TS" a type species that has been determined either by monotypy or by designation in *Index Nominum Genericorum Plantarum* (Farr *et al.*, 1979) or the cited reference. The currently acceptable family designation is followed by the assignment used in a current flora, monographic treatment, or general reference, as cited. Generally the author making the combination can be the point of further reference, with the place of publication available in *Index Kewensis* if not indicated.

The herbarium specimens I have seen are cited BM, LINN-SM with a number, P-A with a number (Adanson), P-J with a number (Jussieu), and P-R with a volume and folio number (Rousseau). A few of the specimens attributed in the literature to the British Museum were on loan and could not be verified. I was able to examine the complete Rousseau herbarium and those bundles of the Jussieu herbarium from which Aublet specimens were cited in the index, but only a very few bundles of the Adanson herbarium. The last often contained the most complete specimens, occasionally with extensive holographic notes. The Adanson collection (loose specimens in folders in bundles) should be consulted before any other specimen is automatically considered for lectotypification. The Aublet specimens appeared to be in folders containing an undeciphered numbering system on the upper right-hand corner of the face of the folder. The extensive spirit collection at the British Museum was not examined but is known to contain fruiting material associated with some of Aublet's specimens. Aublet's notes obtained by Sir Joseph Banks and bound separately are not complete; the missing ones should be sought in the Adanson herbarium. The original drawings (BM) are also bound separately and do not constitute a complete set. The drawings do not always match the final engraved plate, and the fruits, flowers, or dissections may be on separate sheets of paper, suggesting that the mixtures reported for some plates may be due to errors in supplying drawings to the engravers.

ALPHABETIC LISTING OF THE AUBLET PLATES

ABEREMOA GUIANENSIS (**1:** 610. *t. 245* (*guyannensis*))—NG, TS—Annonaceae = **Guatteria guianensis** (Aublet) R. Fries. *Duguetia* St. Hil. is a conserved generic name (#2680), with the type (*D. lanceolata* St. Hil.) not conserved; *Aberemoa* Aublet is listed as rejected. Fries transferred the single species *Aberemoa guianensis* Aublet to *Guatteria* but has also described *Duguetia guianensis* R. Fries as a distinct species. In a key Hutchinson (1964, p. 78) distinguished *Duguetia* as having the carpels sessile or nearly so in fruit and the indumentum stellate or lepidote (as appears to be the case in Aublet's *plate 245*), while *Guatteria* has the carpels more or less stipitate in fruit. If *Aberemoa guianensis* is a species of *Guatteria*, then Aublet's name need not be listed as a *nomen rejiciendum*. A sterile specimen (BM) cannot be placed to genus. However, when Dunal (Monogr. Annon. 126. 1817) published *Guatteria aberemoa* based on the Aublet description and plate, he stated that a specimen at P was the Aublet species but with a smaller, short, stipitate fruit. If Aublet's *Aberemoa guianensis* is indeed a species of *Duguetia*, a new specific name is required.

ABLANIA GUIANENSIS (**1:** 585. *t. 234* (*guyannensis*))—NG, TS—Elaeocarpaceae = **Sloanea guianensis** (Aublet) Bentham. Bentham did not cite specimens in making the transfer to *Sloanea*. BM, LINN-SM 962.1.

ABUTA AMARA (**1:** 620. *t. 251*)—Aristolochiaceae = **Aristolochia glaucescens** H.B.K. Jackson (Index Kew. **1:** 4. 1893) listed *Abuta amara* as equaling *Aristolochia glaucescens.* The Aublet plate illustrates a sterile specimen, seemingly an *Aristolochia* but clearly not a species of *Abuta* (Menispermaceae). Lemée (1955, p. 549) accepted this assignment credited to "I.K." and later (1956, p. 32) noted that he had seen a herbarium specimen. The Aublet name "amara" is older, and a transfer and a new combination in *Aristolochia* are necessary if herbarium material can be located and does verify the identification. Specimens could not be located at BM or P.

ABUTA RUFESCENS (**1:** 618. *t. 250*)—NG, TS—Menispermaceae = **Abuta rufescens** Aublet. For notes on the lectotypification of Aublet specimens, see Barneby and Krukoff (Mem. New York Bot. Gard. **22**(2): 37–40. 1971). Specimen at BM marked "holotype" by Barneby and Krukoff; LINN-SM 1554.16; P-J 10831.

ACIOA GUIANENSIS (**2:** 698. *t. 280* (*guyannensis*))—NG, TS—Chrysobalanaceae = **Acioa guianensis** Aublet. BM.

ACOUROA VIOLACEA (**2:** 753. *t. 301*)—NG, TS—Leguminosae. *Dalbergia* L. f. is a conserved name (#3821), with the type species *D. lanceolaria* L. f. (not conserved; from Sri Lanka); *Acouroa* Aublet is listed as rejected. No modern disposition of the Guianan *Acouroa violacea* Aublet has been located. BM (not found).

ADIANTUM GUIANENSE (**2:** 963. *t. 365* (*guyannense*))—Lindsaeaceae = **Lindsaea guianensis** (Aublet) Dryander. Specimen at BM marked "type."

ADIANTUM SAGITTATUM (**2:** 964. *t. 366* (*sagitatum*))—Lindsaeaceae = **Lindsaea sagittata** (Aublet) Dryander. Kramer (Acta Bot. Neerl. **6:** 260. 1957) annotated a specimen at BM as isotype but did not see a specimen at P that he felt would be the holotype.

AIOUEA GUIANENSIS (**1:** 311. *t. 120* (*guyannensis*))—NG, TS—Lauraceae = **Aiouea guianensis** Aublet. In 1973 Kostermans annotated P-J 4260 as the isotype. Renner (Fl. Neotrop. **31:** 110. 1982) cited "holotype, BM."

AMAIOUA GUIANENSIS (Suppl. 13. *t. 375* (*guyannensis*))—NG, TS—Rubiaceae = **Amaioua guianensis** Aublet. Specimen at BM labeled "type."

AMANOA GUIANENSIS (**1:** 256. *t. 101* (*guyannensis*))—NG, TS—Euphorbiaceae = **Amanoa guianensis** Aublet. BM, P-R 6: 229.

AMBELANIA ACIDA (**1:** 266. *t. 104*)—NG, TS—Apocynaceae = **Ambelania acida** Aublet. Specimen at BM marked "holotype"; LINN-SM 440/1; P-R 7: 242.

ANIBA GUIANENSIS (**1:** 327. *t. 126* (*guyannensis*))—NG, TS—Lauraceae = **Aniba guianensis** Aublet. Kubitzki (Fl. Neotrop. **31:** 45. 1982) cited "holotype BM, isotype C."

ANNONA AMBOTAY (**1:** 616. *t. 249*)—Annonaceae = **Annona ambotay** Aublet. BM, LINN-SM 983.5.

ANNONA LONGIFOLIA (**1:** 615. *t. 248*)—Annonaceae = **Fusea longifolia** (Aublet) Saff. BM, P-J 10770.

ANNONA PALUDOSA (**1:** 611. *t. 246*)—Annonaceae = **Annona paludosa** Aublet. BM, LINN-SM 983.4, P-J 10771.

ANNONA PUNCTATA (**1:** 614. *t. 247*)—Annonaceae = **Guatteria punctata** (Aublet) Howard, comb. nov. Robert Fries (Acta Horti Berg. **10:** 314. 1931) suggested *Annona punctata* Aublet was a *Guatteria,* but he did not make the combination. Later (*Ibid.* **12:** 434. 1939) he listed "*Annona punctata* Aublet Pl. Guian. franc. 1 (1775) 614, tab. 247 (fruct. excl.)" as a synonym of *Guatteria chrysopetala* (Steudel) Miq., which is based on *A. chrysopetala* Steudel (Flora **26:** 754. 1843). Lemée (1956, p. 34) also accepted this assignment. A new combination in *Guatteria* is required for the earlier basionym. BM.

APALATOA SPICATA (**1:** 383. *t. 147* (*Opalatoa*))—NG, TS—Leguminosae = **Crudia spicata** (Aublet) Willd. Robert Williams (Fl. Trinidad Tobago **1:** 256. 1931) determined that "Aubl. t. 147, F 56 [error for 5, 6]" is *Pterocarpus rohrii* Vahl. *Crudia spicata* (Aublet) Willd. is therefore typified by the flowering specimen in the plate, excluding the fruit and seed shown. BM, LINN-SM 743.1.

APEIBA ASPERA (**1:** 545. *t. 216*)—Tiliaceae.
According to Uittien (*in* Pulle, 1932, **3**(1): 52, 53, 440), the fruit (*fig. 2*) is that of *Apeiba echinata* Gaertner, and the flowering branch is referred to *Apeiba glabra* Aublet. Farr *et al.* (1979, p. 107) state that a type species has not been designated for *Apeiba.* The genus is currently under study by Meijer, who will make a designation. BM.

APEIBA GLABRA (**1:** 541. *t. 214* (*laevis*))—Tiliaceae = **Apeiba glabra** Aublet. BM, LINN-SM 929.6.

APEIBA PETOUMO (**1:** 543. *t. 215*)—Tiliaceae = **Apeiba petoumo** Aublet. Uittien (*in* Pulle, 1932, **3**(1): 51) cited *A. petoumo* Aublet "but for the fruit" and *A. aspera* Aublet "as to the fruit" in the synonymy of *Apeiba echinata* Gaertner (Fruct. Semin. Pl. **2:** *t. 121.* 1791). Lemée (1952, p. 348) had a similar treatment. Sandwith (1931, p. 180) accepted *Apeiba petoumo* Aublet (excl. fructu) and placed *A. echinata* Gaertner *emend.* Uittien in synonymy. BM.

APEIBA TIBOURBOU (**1:** 538. *t. 213*)—Tiliaceae = **Apeiba tibourbou** Aublet. BM, LINN-SM 929.3.

APOCYNUM ACOUCI (**1:** 274. *t. 107* (*Apocinum*))—Apocynaceae = **Forsteronia acouci** (Aublet) DC. BM, P-R 10: 343.

APOCYNUM UMBELLATUM (**1:** 275. *t. 108*)—Apocynaceae = **Forsteronia umbellata** (Aublet) Woodson. P-R 10: 343.

AROUNA GUIANENSIS (**1:** 16. *t. 5* (*guyannensis*))—NG, TS—Leguminosae = **Dialium guianensis** (Aublet) Sandw. Specimen at BM labeled "type specimen"; LINN-SM 69.1; P-R 1: 33.

ARUBA GUIANENSIS (**1:** 294. *t. 115* (*guyannensis*))—NG, TS—Simaroubaceae = **Simaba guianensis** Aublet. BM, P-R 11: 349.

BACOPA AQUATICA (**1:** 129. *t. 49* (*guyannensis*))—NG, TS—Scrophulariaceae = **Bacopa aquatica** Aublet. BM, LINN-SM 279.1.

BAGASSA GUIANENSIS (Suppl. 15. *t. 376* (*guyannensis*))—NG, TS—Moraceae = **Bagassa guianensis** Aublet. BM.

BAILLIERIA ASPERA (**2:** 804. *t. 317*)—NG, TS—Compositae = **Clibadium surinamense** L. BM, LINN-SM 1340.3.

BANARA GUIANENSIS (**1:** 548. *t. 217* (*guyannensis*))—NG, TS—Flacourtiaceae = **Banara guianensis** Aublet. Specimen at BM annotated "holotype" by Sleumer; LINN-SM 852.1.

BANISTERIA QUAPARA (**1:** 464. *t. 186*)—Malpighiaceae = **Hiraea quapara** (Aublet) Sprague. Niedenzu (Pflanzenr. IV. **141:** 132. 1928) used the name *Hiraea multiradiata* Juss., rejecting the Aublet name on the basis of a mixed plate and excluding the fruit. The flowering branch illustrated by Aublet therefore typifies the species, and Sprague's combination is to be used. BM, LINN-SM 824.3.

BANISTERIA SINEMARIENSIS (**1:** 462. *t. 185*)—Malpighiaceae = **Mascagnia sinemariensis** (Aublet) Griseb. Niedenzu (Pflanzenr. IV. **141:** 113. 1928) noted that the fruit in Aublet's plate had to be excluded. He rejected the Aublet name on the basis of a mixed plate and used the name *Mascagnia volubilis* (Sims) Niedz. (based on *Malpighia volubilis* Sims (1805)). Since Niedenzu typified the Aublet name by excluding the fruit, the combination by Grisebach is appropriate. BM, LINN-SM 824.5.

BASSOVIA SYLVATICA (**1:** 217. *t. 85*)—NG, TS—Solanaceae = **Solanum sylvaticum** (Aublet) Bitter. Lemée (1953, p. 395) accepted *Solanum aubletii* Pulle, although this illegitimate name was placed in synonymy by Bitter in 1921. BM, P-R 5: 189.

BAUHINIA GUIANENSIS (**1:** 377. *t. 145* (*guyannensis*))—Leguminosae = **Bauhinia guianensis** (Aublet). BM.

BAUHINIA OUTIMOUTA (**1:** 375. *t. 144*)—Leguminosae = **Bauhinia guianensis** Aublet. Lemée (1952, p. 85) accepted *Bauhinia rubiginosa* Bong., noting as synonyms "*B. coronata* Benth., peut-être *B. outimoutou* Aubl. selon J. Amshoff: S. Amer. Papil. 31 [1939]." Wunderlin (pers. comm.) considers it to be the same as *B. guianensis* Aublet and designated a "holotype" (W) and an isotype (BM). Wunderlin considers *Bauhinia rubiginosa* Brongn. to be a much different plant. BM.

BEGONIA GLABRA (**2:** 916. *t. 349*)—Begoniaceae = **Begonia glabra** Aublet. Lemée (1953, p. 98) accepted *Begonia scandens* Sw. (when this name was published in 1788, *B. glabra* Aublet (1775) was included as a synonym). BM.

BEGONIA HIRSUTA (**2:** 913. *t. 348*)—Begoniaceae = **Begonia hirsuta** Aublet. BM.

BERTIERA GUIANENSIS (**1:** 180. *t. 69* (*guyannensis*))—NG, TS—Rubiaceae = **Bertiera guianensis** Aublet. Specimen at BM labeled "type"; P-R 8: 272.

BESLERIA COCCINEA (**2:** 632. *t. 255*)—Gesneriaceae = **Drymonia coccinea** (Aublet) Wiehler. LINN-SM 1058.3.

BESLERIA INCARNATA (**2:** 635. *t. 256* (*Beslaria*))—Gesneriaceae = **Rechsteineria incarnata** (Aublet) Leeuwenberg. Specimen at BM labeled "holotype" by

Leeuwenberg but annotated *Sinningia incarnata* (Aublet) Denham by Wiehler in 1976.

BESLERIA VIOLACEA (**2:** 630. *t. 254* (*Beslaria*))—Bignoniaceae = **Schlegelia violacea** (Aublet) Griseb. BM.

BIGNONIA ALBA (**2:** 653. *t. 266*)—Bignoniaceae = **Memora alba** (Aublet) Miers. Sandwith (Candollea **7:** 251. 1937) called *Bignonia alba* a "nomen dubium" and concluded that it "must certainly not be identified with *Memora bracteosa*." Jackson (Index Kew. **1:** 303. 1893) had referred *Bignonia alba* to *Spathodea bracteosa* DC., which was transferred to *Macfadyena bracteosa* by Bentham and Hooker (Gen. Pl. **2:** 1035). *Memora bracteosa* (DC.) Bur. ex K. Schum. was accepted by Pulle (Fl. Suriname **4**(2): 51. 1938), without the citation of *B. alba*. Alwyn Gentry (pers. comm.) accepts *Memora alba* (Aublet) Miers as a "perfectly good species closely related to *M. flavida*. There is even a type specimen at the British Museum. It consists only of a leaf but looks like a good match for the illustration. It is probable that Sandwith had never seen material of this taxon, but it has recently been re-collected twice by Oldeman. . . . In my opinion there is really nothing dubious about it at all." Specimen at BM labeled "type" by A. Gentry.

BIGNONIA COPAIA (**2:** 650. *t. 265*)—Bignoniaceae = **Jacaranda copaia** (Aublet) D. Don. BM material on loan.

BIGNONIA ECHINATA (**2:** 648. *tt. 263, figs. 1, 2; 264*)—Bignoniaceae. Alwyn Gentry (Ann. Missouri Bot. Gard. **60:** 910. 1973) noted that the fruit is *Pithecoctenium echinatum* (Jacq.) Baillon, while the leaves and flowers are *Arrabidaea inaequalis* (DC. ex Splitg.) K. Schum. BM.

BIGNONIA FLUVIATILIS (**2:** 655. *t. 267*)—Bignoniaceae. Sandwith (Rec. Trav. Bot. Néer. **34:** 225. 1937) noted, "the wisest course is to treat his name [*B. fluviatilis*] as *nomen dubium*." However, Sandwith (*in* Pulle, 1938, **4**(2): 69) listed *B. fluviatilis* Aublet in the synonymy of *Tabebuia aquatilis* (E. Meyer) Sprague and Sandwith "*partim*." No specimen located at BM.

BIGNONIA INCARNATA (**2:** 645. *tt. 261, 262*)—Bignoniaceae = **Mansoa kerere** (Aublet) A. Gentry var. **incarnata** (Aublet) A. Gentry. Sandwith (Meded. Bot. Mus. Utrecht **40:** 205. 1937) discovered discordant elements in the description, plates, and specimens of Aublet and recommended a status of *nomen dubium*. He listed (*in* Pulle, 1938, **4**(2): 28) *B. incarnata* as a synonym of *Cydista aequinoctialis* (L.) Miers. Alwyn Gentry (Ann. Missouri Bot. Gard. **60:** 890. 1973) listed the Aublet name as a synonym of *Pachyptera kerere* (Aublet) Sandwith but later (*Ibid.* **66:** 783. 1979) recognized the variety. He did not see a type specimen.

BIGNONIA KERÉRÉ (**2:** 644. *t. 260* (*cherere*))—Bignoniaceae = **Mansoa kerere** (Aublet) A. Gentry. Sandwith (Meded. Bot. Mus. Utrecht **34:** 219. 1937) discussed the "faulty and deficient" description of the Aublet species and excluded the description of the fruit and *figures 1–4* of *plate 263*. Alwyn Gentry (Ann. Missouri Bot. Gard. **66:** 783. 1979) proposed the assignment recognized here and cited *Aublet s.n.* (BM, P-A 12271, W) without designating a lectotype. LINN-SM 1048.5.

BLAKEA QUINQUE-NERVIA (**1:** 525. *t. 210*)—Melastomataceae = **Bellucia grossularioides** (L.) Triana. BM, LINN-SM 853.1.

BOCOA PROUACENSIS (Suppl. 38. *t. 391* (*provassensis*))—NG, TS—Leguminosae = **Bocoa prouacensis** Aublet. Richard Cowan (Proc. Biol. Soc. Washington **87:** 95–128. 1974) accepted the genus *Bocoa* and published a revision. He indicated that the "type collection" is *Aublet s.n.* (BM). Such a specimen (BM) is annotated "holotype" by Cowan.

BOMBAX GLOBOSA (**2:** 701. *t. 281*)—Bombacaceae = **Eriotheca globosa** (Aublet) Robyns. Robyns (Bull. Jard. Bot. Bruxelles **33:** 124. 1963) cited the Aublet plate as the holotype. No specimens have been located.

BUTTNERIA SCABRA (**1:** 241. *t. 96*)—Sterculiaceae = **Byttneria scabra** L. BM, P-J 12464, P-R 5: 171.

CABOMBA AQUATICA (**1:** 321. *t. 124*)—NG, TS—Cabombaceae = **Cabomba aquatica** Aublet. P-J 3194.

CACAO GUIANENSIS (**2:** 683. *t. 275* (*guyannensis*))—Sterculiaceae = **Theobroma guianense** (Aublet) Gmelin. Cuatrecasas (Contr. U. S. Natl. Herb. **35:** 379–614. 1964) published a taxonomic revision of the genus *Theobroma.* Under rejected names and excluded species (pp. 586, 587) he summarized earlier notes in his paper, stating, "Consequently, *Cacao guianensis* Aublet is not a true species, but a mixture of three species. Therefore the Aublet 'species' and name has to be rejected as 'nomen confusum' (articles 63 (3), 65, and 66 of the Code of Nomenclature). The name *Theobroma guianense* has never been consistently used in monographs and general books for any known species." He had noted (*Ibid.*, p. 586), "The flowers were described from specimens of *Theobroma cacao* L.; the branches and leaves from *T. subincanum* Martius. . . . The illustration of this fruit (*Pl. 275, figs. 16 & 17*) agrees unmistakably well with only one recent collection of *Theobroma* fruits, namely that from French Guiana by Benoist, which is the type of *T. velutinum* Benoist. . . . At the British Museum there are preserved Aublet specimens and among them type specimens of *Cacao guianensis* which are syntypes. In 1954, I could identify by close examination an herbarium sheet (with foliage, one flower and an immature fruit) as belonging to *T. subincanum* Mart.; this specimen agrees with the description and drawings given by Aublet for the leaves and branchlets; this evidence could easily incline us to use this specimen as lectotype for *C. guianensis.* But in the carpological collection of the British Museum there is a fragmentary fruit, also a syntype of Aublet's species, which belongs to *T. cacao.*" Cuatrecasas has clearly lectotypified *Cacao guianensis* Aublet by the leaves and branches of the specimen at BM and has excluded the flowers and fruit of Aublet's *plate 275.* The name *Theobroma guianense* (Aublet) Gmelin should be used.

CACAO SYLVESTRIS (**2:** 687. *t. 276*)—Sterculiaceae = **Theobroma sylvestris** (Aublet) Martius. Cuatrecasas (*Ibid.*, p. 387) stated, "*Cacao sylvestris* was pictured from concordant parts of foliage and fruit which agree well with the species at present known as *T. subincanum,* but the flowers mentioned in his description were taken from *T. cacao.*" Later (pp. 563, 564) in the same work, Cuatrecasas considered *Theobroma subincanum* Martius (*in* Buchner, Repert. Pharm. **35:** 23. 1830) and listed as synonyms *Cacao sylvestris* Aublet and *Cacao guianensis* Aublet "pro parte (*tantum folia*)." It appears that *Cacao sylvestris* can be typified by the foliage and that the flowers should be excluded; the specific epithet "sylvestris" should be used. BM, LINN-SM 1237.2.

CACOUCIA COCCINEA (**1:** 450. *t. 179*)—NG, TS—Combretaceae = **Combretum cacoucia** (Baillon) Exell, not *Combretum coccineum* Lam. (1785). BM, P-J 13637.

CALINEA SCANDENS (**1:** 556. *t. 221*)—NG, TS—Dilleniaceae = **Doliocarpus spraguei** Cheeseman, not *D. scandens* Poiret (1812). BM, LINN-SM 911.1.

CAMERARIA TAMAQUARINA (**1:** 260. *t. 102*)—Apocynaceae = **Malouetia tamaquarina** (Aublet) DC. BM, LINN-SM 448.1, P-R 6: 225.

CANANGA OUREGOU (**1:** 608. *t. 244*)—NG, TS—Annonaceae = **Guatteria ouregou** (Aublet) Dunal. *Cananga* (A. P. de Candolle) Hooker & Thomson is a conserved generic name (#2684), and *Cananga* Aublet is rejected. Robert Fries (Acta Horti Berg. **12:** 352. 1939) accepted Dunal's combination. Specimen at BM annotated as *Guatteria podocarpa* Dunal, which was published later.

CARAIPA ANGUSTIFOLIA (**1:** 562. *t. 224, fig. 4* (*angustifolia*))—Chrysobalanaceae = **Couepia** spp. Kubitzki (Mem. New York Bot. Gard. **29:** 131. 1978) noted that Prance suggested the correct generic placement, but neither was able to place the Aublet name to species. Specimen at BM annotated *Couepia* sp. aff. *caryophylloides* R. Br. by Prance.

CARAIPA LATIFOLIA (**1:** 561. *t. 224, fig. 3*)—Chrysobalanaceae = **Licania membranacea** Sagot ex Lanessan, not *L. latifolia* Bentham. Kubitzki (Mem. New York Bot. Gard. **29:** 131. 1978) suggested this placement. BM.

CARAIPA LONGIFOLIA (**1:** 561. *t. 223, fig. 3*)—Chrysobalanaceae = **Licania alba** (Bernoulli) Cuatr., not *Licania longifolia* Benoist. Kubitzki (Mem. New York Bot. Gard. **29:** 131. 1978) suggested this placement. See also Sandwith (Kew Bull. **1931:** 373; **1942:** 53). BM.

CARAIPA PARVIFOLIA (**1:** 561. *t. 223, fig. 1*)—NG, TS—Bonnetiaceae = **Caraipa parvifolia** Aublet. Kubitzki (Mem. New York Bot. Gard. **29:** 122. 1978) designated the specimen with fruit at P as the holotype; the other specimens he saw (BM, G) were only leaves.

CARAPA GUIANENSIS (Suppl. 32. *t. 387* (*guyannensis*))—NG, TS—Meliaceae = **Carapa guianensis** Aublet. Specimen at BM marked "holotype."

CARAPICHEA GUIANENSIS (**1:** 168. *t. 64* (*guyannensis*))—NG, TS—Rubiaceae = **Psychotria ligularis** (Rudge) Steyerm. var. **carapichea** (Poiret) Steyerm., not *Psychotria guianensis* Raeuschel. *Cephaëlis* Sw. is a conserved generic name (#8411), and *Carapichea* Aublet is rejected. Steyermark considered *Cephaëlis* a synonym of *Psychotria.* BM, P-R 8: 265.

CARICA SPINOSA (**2:** 908. *t. 346*)—Caricaceae = **Jacaratia spinosa** (Aublet) DC. BM.

CASSIA APOUCOUITA (**1:** 379. *t. 146*)—Leguminosae = **Cassia apoucouita** Aublet. Specimen at BM marked "type."

CASSIPOUREA GUIANENSIS (**1:** 529. *t. 211* (*guyannensis*))—NG, TS—Rhizophoraceae = **Cassipourea guianensis** Aublet. BM.

CATINGA AROMATICA (**1:** 512. Index, p. 6 (*Catringa*). *t. 203, figs. 2, 3*)—Myrtaceae = **Eugenia feijoa** Berg. See McVaugh (Mem. New York Bot. Gard. **18:** 181–183. 1969) for discussion. No supporting specimens were located.

CATINGA MOSCHATA (**1:** 511. Index, p. 6 (*Catringa*). *t. 203, fig. 1*)—NG, TS—Myrtaceae = ? **Calycorectes bergii** Sandwith. For discussion of this taxon, see Sandwith (Kew Bull. **1932:** 212. 1932) and McVaugh (Mem. New York Bot. Gard. **18:** 222. 1969). No supporting specimens were located.

CHRYSOPHYLLUM MACOUCOU (**1:** 233. *t. 92*)—Sapotaceae.
Although Lemée (1953, p. 256; 1956, p. 95) accepted this species, Cronquist (Bull. Torrey Bot. Club **73:** 311. 1946) had called it a *nomen confusum* based "on fruit of *Chrysophyllum cainito* and foliage of some other plant." BM (sterile specimen clearly not a *Chrysophyllum*).

CIPONIMA GUIANENSIS (**1:** 567. *t. 226* (*Siponima guyannensis*))—NG, TS—Symplocaceae = **Symplocos guianensis** (Aublet) Gürcke. BM, LINN-SM 1245.3.

CIPURA PALUDOSA (**1:** 38. *t. 13*)—NG, TS—Iridaceae = **Cipura paludosa** Aublet. BM material on loan, but a specimen was photographed by Meyer (#4059); P-R 1: 52.

CLEOME GUIANENSIS (**2:** 675. *t. 273* (*guyannensis*))—Capparaceae = **Cleome guianensis** Aublet. P-J 11227.

COFFEA GUIANENSIS (**1:** 150. *t. 57* (*guyannensis*))—Rubiaceae = **Faramea** sp.? Lemée (1953, p. 540) listed the Aublet name as a synonym under a questionable and undesignated species of *Faramea.* This cannot be *Faramea guianensis* (Aublet) Bremek., which has as a basionym *Evea guianensis* Aublet. BM, P-R 6: 211 labeled "type."

COFFEA PANICULATA (**1:** 152. *t. 58*)—Rubiaceae.
Lemée (1953, p. 542) listed this as "*Coussarea paniculata* ?," but he also cited *Coussarea paniculata* (Vahl) Standley. The Aublet name is not placed satisfactorily. BM, P-R 6: 211.

COMBRETUM LAXUM (**1:** 351. *t. 137*)—Combretaceae = **Combretum rotundifolium** Rich., not *Combretum laxum* Jacq. BM.

COMMELINA HEXANDRA (**1:** 35. *t. 12*)—Commelinaceae = **Dichorisandra hexandra** (Aublet) Standley. P-R 1: 49.

CONAMI BRASILIENSIS (**2:** 927. *t. 354*)—NG, TS—Euphorbiaceae = **Phyllanthus brasiliensis** (Aublet) Oken. BM.

CONCEVEIBA GUIANENSIS (**2:** 924. Index, p. 9 (*Couceveiba*). *t. 353* (*Couceveiba guyannensis*))—NG, TS—Euphorbiaceae = **Conceveiba guianensis** Aublet. BM.

CONOBEA AQUATICA (**2:** 639. *t. 258*)—NG, TS—Scrophulariaceae = **Conobea aquatica** Aublet. BM.

CONOHORIA FLAVESCENS (**1:** 239. *t. 95*)—NG, TS—Violaceae = **Rinorea flavescens** (Aublet) Kuntze. See Sandwith (1931, p. 172). Specimen at BM labeled "holotype"; P-R 5: 172 labeled "type" by Hekking.

CONVOLVULUS GLABER (**1:** 138. *t. 53*)—Convolvulaceae = **Merremia glaber** (Aublet) Hallier f. P-R 6: 197.

CONVOLVULUS GUIANENSIS (**1:** 136. *t. 52* (*guyannensis*))—Convolvulaceae = **Jacquemontia guianensis** (Aublet) Meisner (as *guyanensis*). No supporting specimens located.

CORDIA COLLOCOCA (**1:** 219. *t. 86* (*collo-cocus*))—Boraginaceae = **Cordia nodosa** Lam., not *C. collococca* L. Lamarck cited Aublet, *t. 86,* and indicated that material from Richard had been included in the original description of *Cordia nodosa.* BM, LINN-SM 374.5, P-R 5: 181.

CORDIA FLAVESCENS (**1:** 226. *t. 89*)—Lauraceae.
Ivan Johnston (Jour. Arnold Arb. **16:** 44. 1935) noted that this species was based on mixed material of *Cordia* (Boraginaceae) and *Ocotea* (Lauraceae) and rejected the name. *Figures 1–3* represent a *Cordia.* The specimens he saw (BM, S) represented only *Ocotea.* Clearly this name represents some species of the Lauraceae not used in Pulle or Lemée. The BM specimen was not located, although it was photographed by Meyer (#3784). LINN-SM 374.6 consists of foliage plus one fruit and several calyces, which might be identified by a specialist on the Lauraceae.

CORDIA TETRANDRA (**1:** 222. *t. 87*)—Boraginaceae = **Cordia tetrandra** Aublet. BM, P-R 5: 181.

CORDIA TETRAPHYLLA (**1:** 224. *t. 88*)—Combretaceae = **Buchenavia tetraphylla** (Aublet) Howard, comb. nov. Ivan Johnston (Jour. Arnold Arb. **16:** 45. 1935) stated that the description is based on a mixture of "flowers of some species of *Cordia* and the leafy fruiting branches of *Buchenavia capitata* (Combretaceae) and so the name is to be rejected." The plate clearly illustrates a stem of *Buchenavia capitata* showing sympodial branching. Only *figures 1–3,* showing flowers "of some species of *Cordia,*" need to be excluded. *Buchenavia capitata* (Vahl) Eichler was based on *Bucida capitata* Vahl (1796). Regrettably, no material was located, so the Aublet plate (excluding the flowers) represents the lectotype.

CORDIA TOQUÉVÉ (**1:** 228. *t. 90*)—Boraginaceae = **Cordia toqueve** Aublet. Specimen at BM annotated by I. M. Johnston as *Cordia heterophylla* Willd. and filed under that name. Later (Jour. Arnold Arb. **16:** 21. 1935) Johnston recognized *Cordia toqueve* Aublet and indicated that *C. heterophylla* Willd. was a synonym. P-R 5: 181.

COUBLANDIA FRUTESCENS (**2:** 937. *t. 356*)—NG, TS—Leguminosae = **Muellera frutescens** (Aublet) Standley. *Muellera* L. f. (1781) is a conserved generic name (#3837), and *Coublandia* Aublet is rejected. However, the type species of *Muellera monoliformis* L. f. is not conserved, and the necessary combination was made by Standley in 1933. This correction is not in the list of conserved names in the Rules of Nomenclature. Bentham (Jour. Linn. Soc. Bot. **4**(Suppl.): 117. 1860) stated, "*Coublandia frutescens* Aublet Pl. Guian. t. 356 & fr. in t. 300 sub Dugueliae pictus." I doubt if the fruit drawn in *plate 300* is indeed *Muellera frutescens.* BM, LINN-SM 1225.2.

COUEPIA GUIANENSIS (**1:** 519. *t. 207* (*guyannensis*))—NG, TS—Chrysobalanaceae = **Couepia guianensis** Aublet. BM.

COUMA GUIANENSIS (Suppl. 39. *t. 392* (*guyannensis*))—NG, TS—Apocynaceae = **Couma guianensis** Aublet. BM.

COUMAROUNA ODORATA (**2:** 740. *t. 296* (*odora*))—NG, TS—Leguminosae = **Dipteryx odorata** (Aublet) Willd. *Dipteryx* Schreber is a conserved generic name (#3845), and *Coumarouna* Aublet is rejected. The conserved type species is *Dipteryx odorata* (Aublet) Willd. BM, LINN-SM 1177.2.

COUPOUI AQUATICA (Suppl. 16. *t. 377*)—NG, TS—Rubiaceae = **Duroia aquatica** (Aublet) Bremek. The generic name *Duroia* L. f. is conserved (#8316) against *Pubeta* L. Aublet did not give a specific epithet in the description of the genus but did in the Index (p. 9) and on the plate. Miers (Apocyn. S. America, p. 15. 1878) recognized the discordant elements in the protologue of Aublet and proposed the name *Cupirana aubletiana* Miers for the fruit. Bremekamp (Rec. Trav. Bot. Néerl. **31:** 268–272. 1934), in transferring the specific name to *Duroia,* also discussed the Aublet material and illustration. BM.

COURATARI GUIANENSIS (**2:** 724. *t. 290* (*guyannensis*))—NG, TS—Lecythidaceae = **Couratari guianensis** Aublet. No material was located.

COURIMARI GUIANENSIS (Suppl. 27. *t. 384* (*guyannensis*))—NG, TS—Elaeocarpaceae = **Sloanea** sp. (?). Hallier (1918, p. 24) suggested the identification but did not make the combination. This is not *Sloanea guianensis* (Aublet) Bentham (Jour. Linn. Soc. **5**(Suppl. 2): 69. 1861), which is based on *Ablania guianensis* Aublet. Although C. E. Smith did not consider the Aublet name in his monograph of the New World species of *Sloanea* (Contr. Gray Herb. **175:** 1–112. 1945), he stated (pers. comm.) that the flowers (*figs. 1, 2*), the fruit section (*fig. 3*), and the infructescence are not of a species of *Sloanea.* The material at BM is sterile, and the leaves do not appear to represent a *Sloanea.*

COUROUPITA GUIANENSIS (**2:** 708. *t. 282* (*guyannensis*))—NG, TS—Lecythidaceae = **Couroupita guianensis** Aublet. No supporting material was located.

COUSSAPOA ANGUSTIFOLIA (**2:** 956. *t. 363*)—Moraceae = **Coussapoa angustifolia** Aublet. Specimen at BM annotated "holotype" by Akkermann.

COUSSAPOA LATIFOLIA (**2:** 955. *t. 362*)—NG, TS—Moraceae = **Coussapoa latifolia** Aublet. Specimen at BM annotated "holotype" by Akkermann.

COUSSAREA VIOLACEA (**1:** 98. *t. 38*)—NG, TS—Rubiaceae = **Coussarea violacea** Aublet. BM, P-R 4: 132.

COUTAREA SPECIOSA (**1:** 314. *t. 122*)—NG, TS—Rubiaceae = **Coutarea hexandra** (Jacq.) Schum. P-J 9927.

COUTOUBEA RAMOSA (**1:** 74. *t. 28*)—Gentianaceae = **Coutoubea ramosa** Aublet. P-R 3: 114.

COUTOUBEA SPICATA (**1:** 72. *t. 27*)—NG, TS—Gentianaceae = **Coutoubea spicata** Aublet. P-R 3: 114.

CRENEA MARITIMA (**1:** 523. *t. 209*)—NG, TS—Lythraceae = **Crenea maritima** Aublet. BM, LINN-SM 851.1.

CROTALARIA GUIANENSIS (**2:** 761. *t. 305* (*guyannensis*))—Leguminosae = **Clitoria guianensis** (Aublet) Bentham. Specimen at BM annotated "lectotype" by Fantz.

CROTON GUIANENSE (**2:** 882. *t. 339* (*guyannense*))—Euphorbiaceae = **Croton guianensis** Aublet. BM.

CROTON MATOURENSE (**2:** 879. *t. 338*)—Euphorbiaceae = **Croton matourense** Aublet. BM.

CURATELLA AMERICANA (**1:** 579. *t. 232*)—Dilleniaceae = **Curatella americana** L. BM, LINN-SM 960.1.

CYTISUS VIOLACEUS (**2:** 766. *t. 306*)—Leguminosae = **Eriosema violaceum** (Aublet) G. Don. BM.

DEGUELIA SCANDENS (**2:** 750. *t. 300*)—NG, TS—Leguminosae = **Derris pterocarpus** (DC.) Killip, not *Derris scandens* Bentham. *Derris* Lour. is a conserved generic name (#3838), and *Deguelia* Aublet is rejected. Bentham's comment on the fruit (Jour. Linn. Soc. Bot. **4**(Suppl.): 117. 1860) does not seem valid. BM.

DRACONTIUM PENTAPHYLLUM (**2:** 837. Index, p. 10 (*hexandra*). *t. 326* (*Dracuntium hexandra*))—Araceae = **Anthurium pentaphyllum** (Aublet) G. Don. No supporting specimen located.

ENOUREA CAPREOLATA (**1:** 587. *t. 235*)—NG, TS—Sapindaceae = **Paullinia capreolata** (Aublet) Radlk. No supporting specimen located.

EPERUA FALCATA (**1:** 369. *t. 142*)—NG, TS—Leguminosae = **Eperua falcata** Aublet. Richard Cowan (Smithson. Contr. Bot. **28:** 26. 1975) has commented on the lectotypification. Lectotype at BM (detached inflorescence only).

EUGENIA COUMÉTÉ (**1:** 497. *t. 196* (*comete*))—Myrtaceae = **Myrcia coumete** (Aublet) DC. BM, LINN-SM 883.9.

EUGENIA GUIANENSIS (**1:** 506. *t. 201* (*guyannensis*))—Myrtaceae = **Myrcia guianensis** (Aublet) DC. BM, LINN-SM 883.22, P-J 13882.

EUGENIA LATIFOLIA (**1:** 502. *t. 199*)—Myrtaceae = **Eugenia latifolia** Aublet. See Sandwith (Kew Bull. **1932:** 212). BM, P-J 13920.

EUGENIA MINI (**1:** 498. *t. 197*)—Myrtaceae = **Eugenia biflora** (L.) DC. BM.

EUGENIA MONTANA (**1:** 495. *t. 195*)—Myrtaceae = **Marlierea montana** (Aublet) Amshoff. BM.

EUGENIA SINEMARIENSIS (**1:** 501. *t. 198*)—Myrtaceae.

Lemée (1953, p. 155) listed this taxon in the synonymy of *Eugenia coffeifolia* DC. with a question mark. McVaugh (Mem. New York Bot. Gard.

18(2): 219. 1969) was unable to place the Aublet name without locating a specimen and thought it "unwise to take up the name for the species now called *E. coffeifolia.*" Specimen at BM annotated by Amshoff as *Eugenia arivoa* Aublet and filed in that folder; LINN-SM 883.12.

EUGENIA TOMENTOSA (**1:** 504. *t. 200*)—Myrtaceae = **Myrcia tomentosa** (Aublet) DC. BM.

EUGENIA UNDULATA (**1:** 508. *t. 202*)—Myrtaceae = **Eugenia undulata** Aublet. BM, LINN-SM 883.20, P-J 13921.

EUPATORIUM PARVIFLORUM (**2:** 797. *t. 315*)—Compositae = **Mikania parviflora** (Aublet) Urban. Koster (*in* Pulle, 1938, **4**(2): 126) listed *E. parviflorum* Aublet as a synonym of *Mikana amara* (Vahl) Willd., which is based on *Eupatorium amara* Vahl (1794). Urban (Symb. Antill. **5**: 223. 1907) referred the Barbados plant cited by Vahl to *Eupatorium latifolia* Sm. and accepted Aublet's Guiana plant as distinct. BM.

EUPATORIUM TRIFLORUM (**2**: 795. *t. 314*)—Compositae = **Piptocarpha triflora** (Aublet) A. W. Bennett ex Baker. A type specimen was photographed by Meyer (#3672) but was on loan from the BM in 1982.

EVEA GUIANENSIS (**1**: 100. *t. 39* (*guyannensis*))—NG, TS—Rubiaceae = **Faramea guianensis** (Aublet) Bremek. *Cephaëlis* Sw. is a conserved generic name (#8411), and *Evea* Aublet is rejected. Since *Evea guianensis* Aublet is regarded as a species of *Faramea,* it is not necessary to list *Evea* as a rejected name under *Cephaëlis.* BM, LINN-SM 340.7, P-R 4: 131.

EXACUM GUIANENSE (**1**: 68. *t. 26, fig. 1* (*guyannensis*))—Gentianaceae = **Schultesia guianensis** (Aublet) Malme (as *guyanensis*). P-R 3: 113.

EXACUM TENUIFOLIUM (**1**: 70. *t. 26, fig. 2*)—Gentianaceae = **Curtia tenuifolia** (Aublet) Knobl. Jonker (*in* Pulle, 1935, **4**: 413) said that the detail figures should be excluded. P-R 3: 113.

FAGARA PENTANDRA (**1**: 78. *t. 30*)—Rutaceae = **Zanthoxylum pentandrum** (Aublet) Howard, comb. nov. Lemée (1952, p. 180) accepted the name *Fagara pentandra* and cited *Xanthoxylum hermaphroditum* Willd. (Sp. Pl. **4**: 756) in synonymy. The combination *Zanthoxylum pentandrum* (Aublet) Howard is needed if *Fagara* is not recognized as a distinct genus. P-R 3: 120.

FARAMEA CORYMBOSA (**1**: 102. *t. 40, fig. 1*)—NG, TS—Rubiaceae = **Faramea corymbosa** Aublet. Steyermark designated *Faramea corymbosa* Aublet as the type species for the genus. He apparently did not see any material. BM, P-R 4: 130.

FARAMEA SESSILIFLORA (**1**: 104 (*sessiflora*). Index, p. 12 (*sessiliflora*). *t. 40, fig. 2* (*sessiliflora*))—Rubiaceae = **Faramea sessiliflora** Aublet. BM, LINN-SM 340.9, P-R 4: 130.

FEROLIA GUIANENSIS (Suppl. 7. *t. 372* (*guyannensis*))—NG, TS—Moraceae = **Brosimum rufescens** Taub., not *B. guianense* (Aublet) Huber, which is based on *Piratinera guianensis* Aublet. *Brosimum* Sw. is a conserved generic name (#1957), and *Ferolia* Aublet is rejected. BM.

FOTHERGILLA MIRABILIS (**1**: 441. Index, p. 13 (*admirabilis*). *t. 175* (*mirabilia*))—

Melastomataceae = **Miconia mirabilis** (Aublet) L. O. Williams. Gleason (*in* Pulle, 1935, **3**(1): 243) noted that some copies of *Histoire des Plantes de la Guiane Françoise* used *Tamonea guianensis,* and he accepted *Miconia guianensis* (Aublet) Cogn. without indicating that other copies used *Fothergilla mirabilis* in the text and on the plate. Louis Williams (Fieldiana Bot. **29**: 574, 575. 1963) noted, "In the same work (2: 659, *t. 268.* 1775) he [Aublet] published another *Tamonea* in the Verbenaceae. It seems probable that he 'discovered' that he had described two genera with the name *Tamonea* and changed one of them while the work was going through the press. It seems quite clear that he changed the name of the Melastome to *Fothergilla mirabilis* and that he should be followed in this. Indicative that his intent was this is that the name *Tamonea guianensis* does not appear in the index of scientific names but *Fothergilla mirabilis* does—as *F. admirabilis.*"

Henrey (1975, p. 6) noted that several pages of the original printing were changed, as indicated by the asterisk used in the binder's instructions. This resulted from the replacement of the first *Tamonea* with the name *Fothergilla,* which proves to be a later homonym. Unaltered copies are in the libraries of the British Museum (Natural History) and the Royal Botanic Gardens, Kew, and presumably some are to be found in Paris. Aublet did not change the use of the name *Tamonea* for a member of the Verbenaceae. Schreber (1789, p. 19) substituted the name *Ghinia* for the verbenaceous plant. This Moldenke (Phytologia **47**: 409. 1981) has adopted with the argument, "Regardless of Aublet's later attempt to 'cancel out' the earlier publication by substituting '*Fothergilla*' for it and maintain the name for the verbenaceous group, under the present Code of Botanical Nomenclature he was not justified in so doing. Without formal conservation, the later homonym must be rejected, even though *Miconia* Ruiz & Pavon (1794) has since officially been conserved over the melastomataceous *Tamonea* of Aublet (1775) and in spite of the assertion by Green (1935) that 'The name *Tamonea* Aubl. (Verbenaceae) stands without conservation.'" It can be argued that since *Tamonea* (Melastomataceae) is a rejected name, this clears the way for *Tamonea* to be used in the Verbenaceae, as Aublet clearly intended—or that the name *Tamonea* (Melastomataceae) was not validly published because it was "not accepted by the author in the original publication" (Article 34.1 of the Code). Also overlooked is the fact that Buc'hoz (Pl. Nouv. Découv. p. 9. *t. 7.* 1779) recognized early that *Fothergilla* was a later homonym and proposed the name *Lieutautia mirabilis* (Aublet) Buc'hoz for that species. BM, LINN-SM 782.51.

GALIPEA TRIFOLIATA (**2**: 662. *t. 269*)—NG, TS—Rutaceae = **Galipea trifoliata** Aublet. BM.

GOUPIA GLABRA (**1**: 296. *t. 116*)—NG, TS—Goupiaceae = **Goupia glabra** Aublet. BM, LINN-SM 551.1, P-R 12: 368.

GUAPIRA GUIANENSIS (**1**: 308. *t. 119* (*Quapira guyannensis*))—NG, TS—Nyctaginaceae = **Pisonia guianensis** (Aublet) Howard, comb. nov. Current floras vary in the acceptance of *Guapira* as distinct from *Pisonia* L. P-J 5170 (a poor match for the plate).

GUETTARDA COCCINEA (**1:** 317. *t. 123* (*cocinea*))—Rubiaceae = **Isertia coccinea** (Aublet) Gmelin. P-J 9991.

HERNANDIA GUIANENSIS (**2:** 848. *t. 329* (*guyannensis*))—Hernandiaceae = **Hernandia guianensis** Aublet. Kubitzki (Bot. Jahrb. **89:** 147. 1969) indicated the type at BM, with additional specimens at G and NY.

HEVEA GUIANENSIS (**2:** 871. *t. 335* (*peruviana*))—NG, TS—Euphorbiaceae = **Hevea guianensis** Aublet. BM.

HEYMASSOLI SPINOSA (**1:** 324. *t. 125*)—NG, TS—Olacaceae = **Ximenia americana** L. BM, P-J 11894.

HIRTELLA AMERICANA (**1:** 247. *t. 98* (*Hitella*))—Chrysobalanaceae = **Hirtella racemosa** Lam., not *H. americana* L. P-R 6: 214 marked "type of *H. americana* Aubl."

HOUMIRI BALSAMIFERA (**1:** 564. *t. 225*)—Humiriaceae = **Humiria balsamifera** (Aublet) St.-Hil. *Humiria* Aublet is conserved (#3953), with the spelling correction made by Saint-Hilaire; *Houmiri* Aublet is rejected. BM, LINN-SM 940.1.

HYDROLEA SPINOSA (**1:** 281. *t. 110*)—Hydrophyllaceae = **Hydrolea spinosa** L. LINN-SM 469.3.

HYPERICUM GUIANENSE (**2:** 784. *t. 311* (*Hipericum guyannense*))—Guttiferae = **Vismia guianensis** (Aublet) Choisy. BM.

HYPERICUM LATIFOLIUM (**2:** 787. *t. 312, fig. 1*)—Guttiferae = **Vismia latifolia** (Aublet) Choisy. BM.

HYPERICUM SESSILIFOLIUM (**2:** 787. *t. 312, fig. 2*)—Guttiferae = **Vismia sessilifolia** (Aublet) DC. BM.

ICACOREA GUIANENSIS (Suppl. 1. *t. 368* (*guyannensis*))—NG, TS—Myrsinaceae = **Ardisia guianensis** (Aublet) Mez. The name *Ardisia* Sw. is conserved (#6285), as is the type species *A. tinifolia* Sw.; *Icacorea* Aublet is rejected. Recently, C. L. Lundell (Phytologia **49:** 346. 1981) has reestablished *Icacorea* Aublet as a genus distinct from *Ardisia* Sw. BM.

ICICA ALTISSIMA (**1:** 342. *t. 132*)—Burseraceae = **Tetragastris altissima** (Aublet) Swart. No supporting specimen was located.

ICICA ARACOUCHINI (**1:** 343. *t. 133*)—Burseraceae = **Protium aracouchini** (Aublet) Marchand (as *aracouchili*). BM.

ICICA DECANDRA (**1:** 346. *t. 135* (*pentandra*))—Burseraceae = **Protium decandrum** (Aublet) Marchand. BM.

ICICA ENNEANDRA (**1:** 345. *t. 134*)—Burseraceae = **Protium decandrum** (Aublet) Marchand. BM.

ICICA GUIANENSIS (**1:** 340. *t. 131* (*guyannense*))—Burseraceae = **Protium guianense** (Aublet) Marchand. BM.

ICICA HEPTAPHYLLA (**1:** 337. *t. 130*)—NG, TS—Burseraceae = **Protium hepta-**

phyllum (Aublet) Marchand. Swart (Rec. Trav. Bot. Néerl. **39:** 301. 1942) reported that he could not locate a specimen and regarded the plate as the type. BM.

IROUCANA GUIANENSIS (**1:** 329. *t. 127* (*guyannensis*))—NG, TS—Flacourtiaceae = **Casearia guianensis** (Aublet) Urban. BM.

IVIRA PRURIENS (**2:** 695. *t. 279* (*Iuira*))—NG, TS—Sterculiaceae = **Sterculia pruriens** (Aublet) Schum. BM, LINN-SM 1498.15.

JUSTICIA COCCINEA (**1:** 10. *t. 3*)—Acanthaceae = **Pachystachya coccinea** (Aublet) Nees. BM.

JUSTICIA VARIEGATA (**1:** 12. *t. 4*)—Acanthaceae = **Odontonema variegata** (Aublet) Kuntze. Specimen at BM annotated by V. M. Baum: "Status uncertain, to be removed from *Odontonema*"; P-R 1: 20.

LECYTHIS AMARA (**2:** 716. *t. 286*)—Lecythidaceae = **Eschweilera amara** (Aublet) Niedz. Scott Mori (pers. comm.) accepts this placement, noting, "This is a widespread species to which the name *E. odora* (Poeppig ex Berg) Miers has been most widely applied." No supporting specimen located.

LECYTHIS GRANDIFLORA (**2:** 712. *tt. 283, 284*)—Lecythidaceae = **Eschweilera grandiflora** (Aublet) Sandwith. Scott Mori (pers. comm.) typifies this species on the habit and flowers as illustrated by Aublet: "However, the fruit he describes as of his *L. grandiflora* are really those of *Lecythis tumefacta* Miers." No supporting specimen located.

LECYTHIS IDATIMON (**2:** 721. *t. 289*)—Lecythidaceae = **Lecythis idatimon** Aublet. Scott Mori (pers. comm.) regards this as "a valid name that applies to a species most often misidentified as *Eschweilera amara* (Aublet) Niedenzu." No supporting specimen located.

LECYTHIS PARVIFLORA (**2:** 717. *t. 287*)—Lecythidaceae = **Eschweilera parviflora** (Aublet) Miers. Scott Mori (pers. comm.) accepts this species in *Eschweilera*. BM.

LECYTHIS ZABUCAJO (**2:** 718. *t. 288*)—Lecythidaceae = **Eschweilera** sp. Scott Mori (pers. comm.) will publish the transfer of this species to *Eschweilera*, adding other species to the synonymy. No supporting specimen located.

LICANIA INCANA (**1:** 119. *t. 45*)—NG, TS—Chrysobalanaceae = **Licania incana** Aublet. BM, P-R 6: 204.

LICARIA GUIANENSIS (**1:** 313. *t. 121* (*guyannensis*))—NG, TS—Lauraceae = **Licaria guianensis** Aublet. P-J 17237 marked "type" in annotation by Kostermans.

LIMODORUM GRANDIFLORUM (**2:** 818. *t. 321*)—Orchidaceae = **Cleistes grandiflorum** (Aublet) Schlechter. No supporting specimen located.

LIMODORUM PENDULUM (**2:** 819. *t. 322*)—Orchidaceae = **Dichaea pendula** (Aublet) Cogn. Material on loan from BM.

LISYANTHUS ALATUS (**1:** 204. *t. 80*)—Gentianaceae = **Chelonanthus alatus** (Aublet) Pulle. Maas (pers. comm.) reported the "type" to be at BM. Material of the genus was on loan from BM; LINN-SM 291.4; P-R 7: 258.

LISYANTHUS CAERULESCENS (**1:** 207. *t. 82*)—Gentianaceae = **Irlbachia caerulescens** (Aublet) Griseb. Maas (pers. comm.) reported the "type" to be at BM. LINN-SM 291.5, P-R 7: 258.

LISYANTHUS GRANDIFLORUS Aublet (**1:** 205. *t. 81*)—Gentianaceae = **Chelonanthus alatus** (Aublet) Pulle. Maas (pers. comm.) suggested this synonymy, with the "type" at BM. LINN-SM 291.6, P-R 7: 258.

LISYANTHUS PURPURASCENS Aublet (**1:** 201. *t. 79*)—Gentianaceae = **Chelonanthus** sp. Maas (pers. comm.) indicated that he and a colleague will publish a new combination of the Aublet species in the genus **Chelonanthus**. The "type" is at BM. P-R 7: 258, P-J 6994.

MABEA PIRIRI (**2:** 867. *t. 334, fig. 1*)—NG, TS—Euphorbiaceae = **Mabea piriri** Aublet. BM.

MABEA TAQUARI (**2:** 870. *t. 334, fig. 2*)—Euphorbiaceae = **Mabea taquari** Aublet. BM.

MACAHANEA GUIANENSIS (Suppl. 6. *t. 371* (*guyannensis*))—NG, TS.
This taxon remains unplaced. Albert C. Smith (Brittonia **3:** 552. 1940) concluded that this was not a member of the Hippocrateaceae, which he was monographing. He noted that Jussieu had suggested the Guttiferae, "which seems at least as likely a position as the Hippocrateaceae. Miers (Trans. Linn. Soc. **28:** 378. 1872), on the basis of the type specimen in the herbarium of the British Museum, placed the species in *Clercia*. He should have used Aublet's name, which was earlier than Vellozo's, for his generic group." Lemée (1952, p. 311) used "*Salicia guyanensis* ? (*Clercia* g. Miers, *Macahanea* g. Aubl. d'après I. k.)." Airy Shaw (*in* Willis, 1973, p. 698) was also uncertain, stating, "*Macahanaea* Steud. = *Macahanea* Aubl. = ? *Salacia* L. (Celastraceae)." BM.

MACOUBEA GUIANENSIS (Suppl. 18. *t. 378* (*guyannensis*))—NG, TS—Apocynaceae = **Macoubea guianensis** Aublet. BM.

MACOUCOUA GUIANENSIS (**1:** 88. *t. 34* (*guyannensis*))—NG, TS—Aquifoliaceae = **Ilex guianensis** (Aublet) Kuntze. BM; P-R (material was seen, but ironically I failed to record the volume and folio numbers, as did Lanjouw and Uittien).

MAHUREA PALUSTRIS (**1:** 558. *t. 222*)—NG, TS—Bonnetiaceae = **Mahurea palustris** Aublet. BM.

MAIETA GUIANENSIS (**1:** 443. *t. 176* (*Mayeta guyannensis*))—NG, TS—Melastomataceae = **Maieta guianensis** Aublet. BM, LINN-SM 782.35.

MALANEA SARMENTOSA (**1:** 106. *t. 41*)—NG, TS—Rubiaceae = **Malanea sarmentosa** Aublet. BM, P-R 4: 129.

MALPIGHIA ALTISSIMA (**1:** 455. *t. 181*)—Malpighiaceae = **Byrsonima aubletii** Kosterm., not *M. altissima* Jacq. BM, LINN-SM 822.4.

MALPIGHIA CRASSIFOLIA (**1:** 457. *t. 182*)—Malpighiaceae = **Byrsonima crassifolia** (L.) Kunth. BM.

MALPIGHIA MOUREILA (**1:** 459. *t. 183*)—Malpighiaceae = **Byrsonima crassifolia** (L.) Kunth. BM, LINN-SM 822.3.

MALPIGHIA VERBASCIFOLIA (**1**: 460. *t. 184*)—Malpighiaceae = **Byrsonima verbascifolia** (L.) DC. BM.

MANABEA ARBORESCENS (**1**: 64. *t. 24*)—Verbenaceae = **Aegiphila integrifolia** (Jacq.) Jackson. The genus *Manabea* is credited to Aublet, although no type species was or has been designated. Specimen at BM annotated "type" by Moldenke; P-R 3: 109.

MANABEA LAEVIS (**1**: 66. *t. 25*)—Verbenaceae = **Aegiphila laevis** (Aublet) Gmelin. Specimen at BM annotated "type" by Moldenke; LINN-SM 215.8; P-R 3: 109.

MANABEA VILLOSA (**1**: 62. *t. 23*)—Verbenaceae = **Aegiphila villosa** (Aublet) Gmelin. Specimen at BM annotated "type" by Moldenke; LINN-SM 215.6.

MANAGA GUIANENSIS (Suppl. 2. *t. 369* (*guyannensis*))—NG, TS.

This taxon has not been placed satisfactorily. Albert C. Smith (Brittonia **3**: 553. 1940) stated, "Hallier (Meded. Herb. Rijks. Leiden **35**: 21. 1918) believes that this monotypic genus may be referred to *Salacia,* but I see little reason for such a belief in the original description and plate (which is repeated in Buchoz, Grand. Jard. Univ. *pl. 59.* 1785). Although I am unable to suggest an alternative position for the genus, I believe that it may definitely be excluded from the Hippocrateaceae." Airy Shaw (*in* Willis, 1973, p. 710) refers the genus to *Salacia* L. (Celastraceae) without any indication of doubt. No supporting specimens located.

MAPANIA SYLVATICA (**1**: 47. *t. 17*)—NG, TS—Cyperaceae = **Mapania sylvatica** Aublet. BM, LINN-SM 108.1, P-R 1: 50.

MAPOURIA GUIANENSIS (**1**: 175. *t. 67* (*guyannensis*))—NG, TS—Rubiaceae = **Psychotria mapourioides** DC., not *P. guianensis* Raeuschel. Specimen at BM annotated "holotype"; P-R 8: 269.

MAPROUNEA GUIANENSIS (**2**: 895. *t. 342* (*Mapronnea guyannensis*)—NG, TS—Euphorbiaceae = **Maprounea guianensis** Aublet (Jablonski, Mem. New York Bot. Gard. **17**: 180. 1967, as "*guyanensis*"). BM (two sheets, one marked "type").

MAQUIRA GUIANENSIS (Suppl. 36. *t. 389* (*guyannensis*))—NG, TS—Moraceae = **Maquira guianensis** Aublet. BM.

MARIPA SCANDENS (**1**: 230. *t. 91*)—NG, TS—Convolvulaceae = **Maripa scandens** Aublet. Specimen at BM annotated by Austin; LINN-SM VIII-22; P-R 5: 180.

MATAYBA GUIANENSIS (**1**: 331. *t. 128* (*Mataiba guyannensis*))—NG, TS—Sapindaceae = **Matayba guianensis** Aublet *emend.* Radlk. (excluding the fruit, which is *Swartzia alatum* Willd. = *S. guianensis* (Aublet) Urban). Reitz (Fl. Il. Catarin. Sapindaceae, pt. 1, p. 133. 1980) stated that the type was at P. BM, P-J 11365.

MATELEA LATIFOLIA (**1**: 278. *t. 109, fig. 2*)—Asclepiadaceae = **Matelea palustris** Aublet. BM, P-R 9: 291.

MATELEA PALUSTRIS (**1**: 278. *t. 109, fig. 1*)—NG, TS—Asclepiadaceae = **Matelea palustris** Aublet. BM, P-R 10: 339.

MATOUREA PRATENSIS (**2**: 642. *t. 259* (*guyannensis*))—NG, TS—Scrophulariaceae = **Stemodia pusilla** Bentham. Lemée (**3**: 416) used this name, placing Aublet's taxon in synonymy, and attributed it to *Index Kewensis*. No supporting specimen was located.

MAYACA FLUVIATILIS (**1**: 42. *t. 15* (*Maiaca fluvialis*)—NG, TS—Mayacaceae = **Mayaca fluviatilis** Aublet. BM; LINN-SM XVIII-13; P-R 1: 51 labeled "type."

MAYEPEA GUIANENSIS (**1**: 81. Index, p. 18 (*Mayepa*). *t. 31* (*guyannensis*))—NG, TS—Oleaceae = **Chionanthus guianensis** (Aublet) Stearn. *Linociera* Sw. ex Schreber is a conserved generic name (#6428), and *Mayepea* Aublet is rejected. Stearn (Ann. Missouri Bot. Gard. **63**: 355. 1976) discussed the union of genera under *Chionanthus*. BM, P-R 3: 103.

MAYNA ODORATA (**2**: 921. *t. 352*)—NG, TS—Flacourtiaceae = **Mayna odorata** Aublet. Sleumer (Fl. Neotrop. **22**: 28. 1980) designated a BM specimen as the holotype.

MEBOREA GUIANENSIS (**2**: 825. *t. 323* (*guyannensis*))—NG, TS—Euphorbiaceae. Lanjouw (Euphorb. Surinam, 9. 1931) concluded this is not *Phyllanthus guyanensis* of Mueller-Arg. and stated, "Whether Aublet's plant is a genuine *Phyllanthus* is very difficult to say and must be left undecided." According to Grady Webster (pers. comm.), "The plant seems definitely Euphorbiaceous and probably belongs in the tribe Phyllantheae, but may not belong in *Phyllanthus*. . . . Apparently it has never been re-collected, and until it is the mystery will apparently continue." BM.

MELASTOMA AGRESTIS (**1**: 425. *t. 166*)—Melastomataceae = **Leandra agrestis** (Aublet) Raddi. BM.

MELASTOMA ALATA (**1**: 410. *t. 158*)—Melastomataceae = **Miconia alata** (Aublet) DC. BM.

MELASTOMA AQUATICA (**1**: 430. *t. 169*)—Melastomataceae = **Nepsera aquatica** (Aublet) Naudin. BM, LINN-SM 654.11.

MELASTOMA ARBORESCENS (**1**: 420. *t. 163*)—Melastomataceae = **Loreya arborescens** (Aublet) DC. BM, LINN-SM 782.15.

MELASTOMA BIVALVIS (**1**: 404. *t. 155, fig. a*)—Melastomataceae = **Acisanthera bivalvis** (Aublet) Cogn. BM.

MELASTOMA CACATIN (**1**: 437. *t. 173*)—Melastomataceae.
Cogniaux (*in* Martius, Fl. Brasil. **14**: 518. 1888) listed this as a poorly known species. Aublet's plate shows a sterile specimen. Wurdack (pers. comm.) wrote, "*Melastoma cacatin* is a most frustrating and vegetatively very distinct species. I have seen the Aublet (sterile) material (BM, P) and have modern sterile and fruiting collections from Surinam and French Guiana. The species is either a *Miconia* or *Tococa* (with fair-sized terminal inflorescences), but flowers are needed." BM, LINN-SM 782.71.

MELASTOMA ELEGANS (**1**: 427. *t. 167*)—Melastomataceae = **Clidemia hirta** (L.) D. Don var. **elegans** (Aublet) Griseb. BM, LINN-SM 782.31.

MELASTOMA FLAVESCENS (**1**: 423. *t. 164*)—Melastomataceae = **Henrietella flavescens** (Aublet) Triana. BM.

MELASTOMA GRANDIFLORA (**1:** 414. *t. 160*)—Melastomataceae = **Rhynchanthera grandiflora** (Aublet) DC. BM, LINN-SM 782.30, P-J 14109.

MELASTOMA LAEVIGATA (**1:** 412. *t. 159*)—Melastomataceae = **Miconia prasina** (Sw.) DC., not *Miconia laevigata* (L.) DC. BM, LINN-SM 782.17.

MELASTOMA LONGIFOLIA (**1:** 432. *t. 170*)—Melastomataceae = **Miconia longifolia** (Aublet) DC. BM, LINN-SM 782.16.

MELASTOMA PARVIFLORA (**1:** 433. *t. 171*)—Melastomataceae = **Miconia prasina** (Sw.) DC. BM.

MELASTOMA PURPURASCENS (**1:** 402. *t. 154*)—Melastomataceae = **Aciotis purpurascens** (Aublet) Triana. BM, LINN-SM 782.38.

MELASTOMA RACEMOSA (**1:** 406. *t. 156* (*racemola*))—Melastomataceae = **Miconia racemosa** (Aublet) DC. BM, LINN-SM 782.4.

MELASTOMA RUBRA (**1:** 416. *t. 161*)—Melastomataceae = **Clidemia rubra** (Aublet) Martius. BM, LINN-SM 782.34.

MELASTOMA RUFESCENS (**1:** 408. *t. 157*)—Melastomataceae = **Miconia rufescens** (Aublet) DC. BM, LINN-SM 782.33.

MELASTOMA SCANDENS (**1:** 435. *t. 172*)—Melastomataceae = **Adelobotrys scandens** (Aublet) DC. BM, LINN-SM 782.20.

MELASTOMA SPICATA (**1:** 423. *t. 165*)—Melastomataceae = **Clidemia capitellata** (Bonpl.) D. Don var. **dependens** (D. Don) Macbr., not *C. spicata* D. Don. BM, P-J 14078.

MELASTOMA SUCCOSA (**1:** 418. *t. 162*)—Melastomataceae = **Henriettea succosa** (Aublet) DC. BM, LINN-SM 782.14.

MELASTOMA TRIVALVIS (**1:** 406. *t. 155, fig. b*)—Melastomataceae = **Acisanthera bivalvis** (Aublet) Cogn. BM, LINN-SM 654.3.

MELASTOMA VILLOSA (**1:** 428. *t. 168*)—Melastomataceae = **Desmoscelis villosa** (Aublet) Naudin. BM, LINN-SM 654.4, 654.5.

MIMOSA BOURGONI (**2:** 941. *t. 358*)—Leguminosae = **Inga bourgoni** (Aublet) DC. (as *Burgoni*). BM (two sheets: one with flowers, one with fruit).

MIMOSA GUIANENSIS (**2:** 938. *t. 357* (*guyannensis*))—NG, TS—Leguminosae = **Stryphnodendron guianensis** (Aublet) Bentham. BM.

MINQUARTIA GUIANENSIS (Suppl. 4. *t. 370* (*guyannensis*))—NG, TS—Olacaceae = **Minquartia guianensis** Aublet. Specimen at BM annotated "holotype" by Sleumer.

MONIERA TRIFOLIA (**2:** 731. *t. 293*)—Rutaceae = **Moniera trifolia** Loefl. BM.

MONTIRA GUIANENSIS (**2:** 637. *t. 257* (*guyannensis*))—NG, TS—Loganiaceae = **Spigelia guianensis** (Aublet) Lemée. Although this combination is attributed to Lemée in *Index Kewensis* (Suppl. 12, p. 135. 1959), Lemée (1953, p. 271) cited "*S*[*pigelia*] *guianensis* ? (*Montira* g. Aublet, d'après I. k.)." No supporting specimen located.

MOQUILEA GUIANENSIS (**1:** 521. *t. 208* (*guyannensis*))—NG, TS—Chrysobalanaceae = **Licania guianensis** (Aublet) Griseb. BM.

MORONOBEA COCCINEA (**2:** 789. *t. 313*)—NG, TS—Guttiferae. The illustration of habit and *figures 1–9* show *Moronobea coccinea* Aublet. BM. *Figures a–j* are *Symphonia globulifera* L. f.

MOURERA FLUVIATILIS (**1:** 582. *t. 233* (*fluviatili*))—NG, TS—Podostemonaceae = **Mourera fluviatilis** Aublet. BM, LINN-SM 963.1, P-A 21473.

MOURIRI GUIANENSIS (**1:** 453. *t. 180* (*guyannensis*))—NG, TS—Melastomataceae = **Mouriri guianensis** Aublet. For a discussion of this material, see Morley (Fl. Neotrop. **15:** 171, 172. 1976), who designated as lectotype the fragment in the lower right-hand corner of the sheet (BM); LINN-SM 784.1 is presumed to be an isotype.

MOUROUCOA VIOLACEA (**1:** 142. Index, p. 20 (*Mouroucoua*). *t. 54*)—NG, TS—Convolvulaceae = **Maripa violacea** (Aublet) Ooststr. ex Lanjouw & Uittien. Specimen at BM annotated "type" by Austin; P-R 6: 194.

MOUTOUBEA GUIANENSIS (**2:** 680. *t. 274* (*guyannensis*))—NG, TS—Polygalaceae = **Moutoubea guianensis** Aublet. BM.

MOUTOUCHI SUBEROSA (**2:** 748. *t. 299*)—NG, TS—Leguminosae = **Pterocarpus officinalis** Jacq. Specimen at BM annotated "holotype" by Rudd.

NACIBEA ALBA (**1:** 98. *t. 37, fig. 2*)—Rubiaceae = **Manettia alba** (Aublet) Wernham. BM, P-R 4: 133.

NACIBEA COCCINEA (**1:** 96. *t. 37, fig. 1*)—NG, TS—Rubiaceae = **Manettia coccinea** (Aublet) Willd. BM, LINN-SM 234.2, P-R 4: 133.

NAPIMOGA GUIANENSIS (**1:** 592. *t. 237* (*guyannensis*))—NG, TS—Flacourtiaceae = **Homalium guianense** (Aublet) Oken. Sleumer (Fl. Neotrop. **22:** 60. 1980) designated a specimen at BM as holotype. P-A 16427.

NISSOLIA QUINATA (**2:** 743. *t. 297*)—Leguminosae = **Machaerium quinatum** (Aublet) Sandwith. Aublet did not supply the specific epithet with the generic description, but the epithet is in the index (p. 20) and on the plate. Specimen at BM annotated "holotype?" by Rudd.

NONATELIA LONGIFLORA (**1:** 185. *t. 71*)—Rubiaceae = **Palicourea longiflora** (Aublet) Rich. BM, LINN-SM 333.31, P-R 8: 271.

NONATELIA LUTEA (**1:** 190. *t. 74*)—Rubiaceae = **Palicourea longiflora** (Aublet) Rich. BM, LINN-SM 342.2.

NONATELIA OFFICINALIS (**1:** 182. *t. 70, fig. 1*)—NG, TS—Rubiaceae = **Psychotria officinalis** (Aublet) Sandwith. BM, P-R 8: 271.

NONATELIA PANICULATA (**1:** 184. *t. 70, fig. 2*)—Rubiaceae = **Psychotria paniculata** (Aublet) Raeuschel. BM (specimen filed under *P. flexuosa*).

NONATELIA RACEMOSA (**1:** 186. *t. 72*)—Rubiaceae = **Psychotria racemosa** (Aublet) Raeuschel. P-R 8: 271.

NONATELIA VIOLACEA (**1:** 188. *t. 73*)—Rubiaceae = **Psychotria capitata** Ruiz & Pavon subsp. **amplifolia** (Raeuschel) Steyerm., not *P. violacea* Aublet. P-R 8: 271.

NORANTEA GUIANENSIS (**1:** 554. *t. 220* (*guyannensis*))—NG, TS—Marcgraviaceae = **Norantea guianensis** Aublet. BM.

OCOTEA GUIANENSIS (**2:** 781. *t. 310* (*guyannensis*))—NG, TS—Lauraceae = **Ocotea guianensis** Aublet. BM.

OMPHALEA DIANDRA (**2:** 843. *t. 328*)—Euphorbiaceae = **Omphalea diandra** L. P-J 16283.

ORELIA GRANDIFLORA (**1:** 271. *t. 106*)—NG, TS—Apocynaceae = **Allamanda cathartica** L. LINN-SM 441.1, P-R 6: 223.

OURATEA GUIANENSIS (**1:** 397. *t. 152*)—NG, TS—Ochnaceae = **Ouratea guianensis** Aublet. LINN-SM 931.9.

OUROUPARIA GUIANENSIS (**1:** 177. *t. 68* (*guyannensis*))—NG, TS—Rubiaceae = **Uncaria guianensis** (Aublet) Gmelin. *Uncaria* Schreber is a conserved generic name (#8228), with the type species designated as *U. guianensis* (Aublet) Gmelin; *Ourouparia* Aublet is rejected. BM, P-R 8: 270.

OUTEA GUIANENSIS (**1:** 29. *t. 9* (*guyannensis*))—NG, TS—Leguminosae = **Macrolobium guianense** (Aublet) Pulle. *Macrolobium* Schreber is a conserved generic name (#3517), and *Vouapa* Aublet (q.v.) and *Outea* Aublet are both rejected. The conserved type species is *Macrolobium bifolium* (Aublet) Pers. (based on *Vouapa bifolia* Aublet). Specimen at BM annotated "isotype" by R. Cowan; LINN-SM 77.1; P-R 1: 45.

PACHIRA AQUATICA (**2:** 726. *tt. 291, 292*)—NG, TS—Bombacaceae = **Pachira aquatica** Aublet. BM.

PACOURIA GUIANENSIS (**1:** 269. *t. 105* (*guyannensis*))—NG, TS—Apocynaceae = **Pacouria guianensis** Aublet. *Landolphia* Beauv. is a conserved generic name (#6562), and *Pacouria* Aublet is rejected. Pulle (Enum. Pl. Surinam, p. 379. 1906) published the combination *Landolphia guianensis* (Aublet) Pulle (as *guyanensis*). Pichon (Monogr. Landolphiées, Mém. l'Inst. Fr. d'Afr. Noire **35:** 245. 1953) reestablished *Pacouria* as a segregate of *Landolphia* and stated the type was "JJR [P]." BM, LINN-SM 440.2, P-R 7: 232.

PACOURINA EDULIS (**2:** 800. *t. 316*)—NG, TS—Compositae = **Pacourina edulis** Aublet. BM.

PAGAMEA GUIANENSIS (**1:** 113 (*Pagama*). Index, p. 21 (*Pagamea*). *t. 44* (*guyannensis*))—NG, TS—Rubiaceae = **Pagamea guianensis** Aublet. BM, LINN-SM 340.8, P-R 4: 143.

PALICOUREA GUIANENSIS (**1:** 173. *t. 66* (*guyannensis*))—NG, TS—Rubiaceae = **Palicourea guianensis** Aublet. BM, P-R 8: 268.

PALMA MARIPA (**2:** 974. *frontisp. 1, 2*)—Arecaceae = **Attalea maripa** Martius. Orator Cook (Jour. Wash. Acad. Sci. **30:** 297. 1940) proposed the new genus *Ethnora* for this taxon, with the type species *Ethnora maripa* (Martius) Cook. Since the generic description, although diagnostic, is in English, and there is neither a Latin description nor reference to a previously published one, the name *Ethnora* is illegitimate. The name *Attalea maripa* Martius is validly published.

In the index Aublet grouped other names in the genus *Palma* as "specificum seu Triviale" names, citing a page reference and the numbers within the frontispiece. In the text, however, the specific names of the index are given only as colloquial names of the Caraïbes and are not in parentheses, as was Aublet's custom with other specific names. Cook (*Ibid.*, p. 299) stated, "The four other palms, 'comon,' 'avoira,' 'bache,' and 'zaguenete,' are identified respectively as *Oenocarpus, Astrocaryum, Mauritia* and *Manicaria*. No other palms were illustrated in Aublet's Histoire, though several were briefly described without botanical names." In contrast, the specific name for *Myrtus citrifolia* Aublet is given only in the index, while the text contains a description and reference to a previously published illustration that has been accepted as the type of the species. I cannot accept the several entries under *Palma* as a comparable case and do not believe that Cook's "identifications" to other genera should constitute publication. Urban (1920, pp. 139–141) has named some of the palms associated with the Plumier references Aublet supplied. Aublet's work is of questionable use in typifying these names.

PALOUE GUIANENSIS (**1**: 365. Index, p. 21 (*Palove*). *t. 141* (*guyannensis*))—NG, TS—Leguminosae = **Paloue guianensis** Aublet. Although Meyer photographed an Aublet specimen (#2291), it could not be found at BM.

PAMEA GUIANENSIS (**2**: 946. *t. 359* (*guyannensis*))—NG, TS—Combretaceae = **Terminalia pamea** DC., not *T. guyanensis* Eichler. De Candolle (Prodr. **3**: 13. 1828) cited *Pamea guianensis* but did not transfer the Aublet species. The specimen at BM is annotated "This is a *Buchenavia*" by C. A. Stace and is filed under that genus. The new combination will be published in his forthcoming revision (pers. comm.).

PANAX MOROTOTONI (**2**: 949. *t. 360* (*undulata*))—Araliaceae = **Didymopanax morototoni** (Aublet) Dcne. & Planchon. BM.

PARALEA GUIANENSIS (**1**: 576. *t. 231*)—NG, TS—Ebenaceae = **Diospyros guianensis** (Aublet) Gürcke. Specimen at BM annotated "isotype?" by F. B. White.

PARIANA CAMPESTRIS (**2**: 877. *t. 337*)—NG, TS—Gramineae = **Pariana campestris** Aublet. BM.

PARINARI CAMPESTRIS (**1**: 517. *t. 206*)—NG, TS—Chrysobalanaceae = **Parinari campestris** Aublet. BM, LINN-SM 648.2, P-J 2786.

PARINARI MONTANA (**1**: 514. *tt. 204, 205*)—Chrysobalanaceae = **Parinari montana** Aublet *emend.* Ducke (as to fruit, *t. 205*). The branches and leaves of *plate 204* are *Parinari rodolphii* Huber. Prance (Fl. Neotrop. **9**: 179, 182, 183. 1972) discussed the confusion regarding the Aublet plates and descriptions. BM.

PARIVOA GRANDIFLORA (**2**: 757. *t. 303*)—NG, TS—Leguminosae = **Eperua grandiflora** (Aublet) Bentham. Specimen at BM annotated "holotype" by R. Cowan; P-J 14646B.

PARIVOA TOMENTOSA (**2**: 759. *t. 304*)—Leguminosae = **Crudia tomentosa** (Aublet) Macbr. BM.

PASSIFLORA COCCINEA (**2**: 828. *t. 324*)—Passifloraceae = **Passiflora coccinea** Aublet. P-A 21430, P-J 16665.

PASSIFLORA STIPULATA (**2**: 830. *t. 325*)—Passifloraceae = **Passiflora stipulata** Aublet. P-A 21403.

PASSOURA GUIANENSIS (Suppl. 21. *t. 380* (*guyannensis*))—NG, TS—Violaceae = **Rinorea pubiflora** (Bentham) Sprague & Sandwith, not *R. guianensis* Aublet. No supporting specimen located.

PATABEA COCCINEA (**1**: 111. *t. 43*)—NG, TS—Rubiaceae = **Ixora davisii** Sandwith, not *I. coccinea* L. BM, P-R 3: 127.

PATIMA GUIANENSIS (**1**: 197. *t. 77* (*guyannensis*))—NG, TS—Rubiaceae = **Patima guianensis** Aublet. BM, LINN-SM 341.1, P-R 7: 257.

PAYPAYROLA GUIANENSIS (**1**: 249. *t. 99* (*guyannensis*))—NG, TS—Violaceae = **Paypayrola guianensis** Aublet. BM, P-R 6: 228.

PEKEA BUTIROSA (**1**: 594. *t. 238*)—NG, TS—Caryocaraceae = **Caryocar villosum** (Aublet) Pers. Prance (Fl. Neotrop. **12**: 33. 1973) noted that the identification applied to the fruit and flowers. He was not able to locate a specimen but concluded that the leaves illustrated were not of *Caryocar*. No supporting specimens were located.

PEKEA TUBERCULOSA (**1**: 597. *t. 239*)—Caryocaraceae = **Caryocar nuciferum** L. as to fruit only. Prance (Fl. Neotrop. **12**: 56. 1973) suggested the leaves are like those found in the Bombacaceae or Sterculiaceae. BM, LINN-SM 968.1, 968.2.

PERAMA HIRSUTA (**1**: 54. *t. 18* (*Perana*))—NG, TS—Rubiaceae = **Perama hirsuta** Aublet. BM, P-R 3: 117.

PEREBEA GUIANENSIS (**2**: 953. *t. 361* (*guyannensis*))—NG, TS—Moraceae = **Perebea guianensis** Aublet. No supporting specimens were located.

PIPAREA DENTATA (Suppl. 31. *t. 386*)—NG, TS—Flacourtiaceae = **Casearia commersoniana** Camb., not *C. dentata* Sessé & Moç. BM.

PIRATINERA GUIANENSIS (**2**: 888. *t. 340* (*guyannensis*))—NG, TS—Moraceae = **Brosimum guianense** (Aublet) Huber. *Brosimum* Sw. is a conserved generic name (#1957), and *Piratinera* Aublet is rejected. BM.

PIRIGARA HEXAPETALA (**1**: 490. *t. 193*)—Lecythidaceae = **Gustavia hexapetala** (Aublet) Sm. No supporting specimens were located.

PIRIGARA TETRAPETALA (**1**: 487. *t. 192*)—NG, TS—Lecythidaceae = **Grias tetrapetala** (Aublet) Niedz. Accepted by Lemée (1953, p. 115). LINN-SM 1156.1.

PIRIPEA PALUSTRIS (**2**: 628. *t. 253*)—NG, TS—Scrophulariaceae = **Buchnera palustris** (Aublet) Sprengel. Specimen at BM annotated "type" by Philcox.

PIRIQUETA VILLOSA (**1**: 298. *t. 117*)—NG, TS—Turneraceae = **Piriqueta viscosa** Griseb. P-J 12802 annotated by Arbo; P-R 12: 367.

PITUMBA GUIANENSIS (Suppl. 29 (*Pitumba*). Index, p. 24 (*Pitumba guianensis*). *t. 385* (*guyannensis*))—NG, TS—Flacourtiaceae = **Casearia pitumba** Sleumer, not *C. guianensis* (L. C. Rich.) Urban. Specimen at BM designated the holotype by Sleumer (Fl. Neotrop. **22**: 351. 1980).

POLYGALA TIMOUTOU (**2**: 737. *t. 295*)—Polygalaceae = **Polygala timoutou** Aublet. BM.

POLYGALA VIOLACEA (**2:** 735. *t. 294*)—Polygalaceae = **Polygala violacea** Aublet. LINN-SM 1176.31.

PORAQUEIBA GUIANENSIS (**1:** 123. *t. 47* (*guyannensis*))—NG, TS—Icacinaceae = **Poraqueiba guianensis** Aublet. BM, P-R 5: 176.

POSOQUERIA LONGIFLORA (**1:** 134. *t. 51*)—NG, TS—Rubiaceae = **Posoqueria longiflora** Aublet. BM, P-J 9931, P-R 6: 199.

POSSIRA ARBORESCENS (**2:** 934. *t. 355*)—NG, TS—Leguminosae = **Swartzia arborescens** (Aublet) Pittier. *Swartzia* Schreber is a conserved generic name (#3574), and *Possira* Aublet is rejected. Richard Cowan (Fl. Neotrop. **1:** 181. 1968) cited: "TYPE COLLECTION. *F. Aublet s.n.* (isotype BM), near source of Galibi R., French Guiana." BM.

POTALIA AMARA (**1:** 394. *t. 151*)—NG, TS—Potaliaceae = **Potalia amara** Aublet. The family Potaliaceae has been placed in the Gentianaceae by Fosberg (Smithson. Contr. Bot. **45:** 18, 19. 1980). Specimen at BM annotated "holotype" by Leeuwenberg; P-J 7021.

POUROUMA GUIANENSIS (**2:** 892. *t. 341* (*guyannensis*))—NG, TS—Moraceae = **Pourouma guianensis** Aublet. Specimen at BM photographed by Meyer (#3552) but not located.

POUTERIA GUIANENSIS (**1:** 86. *t. 33* (*guyannensis*))—NG, TS—Sapotaceae = **Pouteria guianensis** Aublet. The fruit is a species of *Sloanea* (Elaeocarpaceae), while the flowers illustrated have been referred to *Labatia pedunculata* (Sapotaceae). Sandwith (1931, p. 477) and Baehni (Candollea **1:** 264. 1942), among many others, have discussed *P. guianensis*. The type specimen consists of a branch with three leaves. BM.

PSIDIUM AROMATICUM (**1:** 485. *t. 191*)—Myrtaceae = **Campomanesia aromatica** (Aublet) Griseb. LINN-SM 881.3.

PSIDIUM GRANDIFLORUM (**1:** 483. *t. 190*)—Myrtaceae = **Campomanesia grandiflora** (Aublet) Sagot. LINN-SM 881.4.

PSYCHOTRIA VIOLACEA (**1:** 145. *t. 55*)—Rubiaceae.
Steyermark (*in* Maguire, 1972, p. 399) stated that "without an examination of the Aublet specimen, it is not possible to state whether *Psychotria violacea* belongs to *Coccocypselum* or *Geophila*." Lanjouw and Uittien (1940, p. 156) referred to a specimen at BM that I could not locate and to P-R 8: 282, which they felt was a good species of *Coccocypselum*. The final decision should be made by a specialist.

QUALEA CAERULEA (**1:** 7. *t. 2*)—Vochysiaceae = **Qualea caerulea** Aublet. Specimen at BM annotated "holotype" by Stafleu.

QUALEA ROSEA (**1:** 5. *t. 1*)—NG, TS—Vochysiaceae = **Qualea rosea** Aublet. Specimen at BM annotated "holotype" by Stafleu.

QUAPOYA PANA-PANARI (**2:** 900. *t. 344*)—Guttiferae = **Clusia pana-panari** (Aublet) Choisy. BM.

QUAPOYA SCANDENS (**2:** 898. *t. 343*)—NG, TS—Guttiferae = **Quapoya scandens** Aublet. BM.

QUARARIBEA GUIANENSIS (**2:** 692. *t. 278* (*guyannensis*))—NG, TS—Bombacaceae = **Quararibea guianensis** Aublet. BM material on loan.

QUEBITEA GUIANENSIS (**2:** 838 (*Quebitea*). Index, p. 25 (*Quebitea guianensis*). *t. 327* (*guyannensis*))—NG, TS—Piperaceae = **Piper humistratum** Görts & Kramer, not *P. guianensis* DC. Steyermark (pers. comm.) suggested this identification. The Aublet name was not mentioned by Yuncker in his comprehensive *The Piperaceae of Northern South America* or by the authors of *P. humistratum.* Aublet's specimen (BM) is sterile, but it and the illustration now seem to be properly placed.

QUIINA GUIANENSIS (Suppl. 19. *t. 379* (*guyannensis*))—NG, TS—Quiinaceae = **Quiina guianensis** Aublet. BM.

RACARIA SYLVATICA (Suppl. 24. *t. 382*)—NG, TS—Sapindaceae = **Talisia sylvatica** (Aublet) Radlk. BM.

RACOUBEA GUIANENSIS (**1:** 590. *t. 236*)—NG, TS—Flacourtiaceae = **Homalium guianense** (Aublet) Oken. BM.

RAPANEA GUIANENSIS (**1:** 121. *t. 46* (*guyannensis*))—NG, TS—Myrsinaceae = **Myrsine guianensis** (Aublet) Kuntze. BM; P-R 6: 203 annotated "lectotype" by Gillis.

RAPATEA PALUDOSA (**1:** 305. *t. 118*)—NG, TS—Rapateaceae = **Rapatea paludosa** Aublet. P-J 3173.

RAPUTIA AROMATICA (**2:** 671. *t. 272*)—NG, TS—Rutaceae = **Raputia aromatica** Aublet. BM.

REMIREA MARITIMA (**1:** 45. *t. 16*)—NG, TS—Cyperaceae = **Mariscus pedunculatus** (R. Br.) T. Koyama, not *Mariscus maritimus* Miq. P-R 1: 56.

RHEXIA LATIFOLIA (**1:** 336. *t. 129, fig. 2*)—Melastomataceae = **Comolia latifolia** (Aublet) Cogn. No supporting specimen located.

RHEXIA VILLOSA (**1:** 334. *t. 129, fig. 1*)—Melastomataceae = **Comolia villosa** (Aublet) Triana. BM, LINN-SM 654.15.

RIANA GUIANENSIS (**1:** 237. *t. 94* (*guyannensis*))—NG, TS—Violaceae = **Rinorea riana** Kuntze, not *R. guianensis* Aublet. BM; P-R 5: 173 annotated "type" by Hekking.

RINOREA GUIANENSIS (**1:** 235. *t. 93* (*guyannensis*))—NG, TS—Violaceae = **Rinorea guianensis** Aublet. Specimen at BM annotated "holotype"; LINN-SM 409.3; P-R 5: 169 annotated "type" by Hekking, who has proposed the conservation of *Rinorea* Aublet against *Conohoria* Aublet (Taxon **31:** 754. 1982).

ROBINIA NICOU (**2:** 771. *t. 308*)—Leguminosae = **Lonchocarpus rufescens** Bentham. Bentham (Jour. Linn. Soc. Bot. **4**(Suppl.): 99. 1860) noted that "the single leaf of Aublet's *Robinia nicou* preserved in the Banksian herbarium resembles this more than any other species." Although flowers are illustrated along with foliage, a specialist on the Leguminosae should decide if a new combination is justified. BM.

ROBINIA PANACOCO (**2:** 768. *t. 307*)—Leguminosae = **Swartzia panacoco** (Aublet) R. Cowan. Sandwith (Kew Bull. **1934:** 358, 359) discussed this problem in considerable detail:

> Aublet described and figured his *Robinia panacoco* from the leaves and stipules of a *Swartzia* and from the flowers and fruit of another genus, probably—as suggested by de Candolle—of a *Lonchocarpus.* Willdenow's description of *Robinia tomentosa* is partly an adaptation of Aublet's and partly based on his (Aublet's) figure, and there is no evidence that he suspected the composite nature of *Robinia panacoco*; the name *Robinia tomentosa* was therefore superfluous and illegitimate. It was de Candolle who first identified the leaves and stipules with those of flowering material of a *Swartzia* collected in French Guiana by Patris, and proceeded to name and figure the plant as *S. tomentosa* DC., and gave a description of the inflorescence in which, unfortunately, no mention was made of the presence or absence of indumentum on the gynoecium. As the vernacular name of Patris' tree was Bois Pagaye blanc, and not Panacoco, de Candolle reasonably rejected the name Panacoco for the species, and accepted Willdenow's epithet which applied to the *Swartzia* foliage. It is not clear whether de Candolle saw Aublet's dried material or merely matched Patris' specimens with the figure and description. At any rate he was correct, for the *Patris* foliage (kindly lent from Geneva) agrees excellently. . .with that of two sheets collected by Aublet, and corresponds sufficiently to the figure and description of the leaves of *Robinia panacoco* in the British Museum Herbarium. The name *Swartzia tomentosa* DC. should therefore be accepted for this foliage, but the Patris collection should be regarded as the type of the species dating from 1825, *Robinia panacoco* Aubl. being treated as a *nomen confusum* and *Robinia tomentosa* Willd. as an illegitimate name.

Unfortunately, *nomina confusa* are no longer recognized in the Code of Botanical Nomenclature. Sandwith clearly typified the Aublet name with the foliage of a *Swartzia* in the herbarium at BM.

Richard Cowan published the combination *Swartzia panacoco* (Aublet) R. Cowan in *Flora Neotropica* (**1:** 32. 1968) and lectotypified it (p. 38) by *F. Aublet s.n.* (BM). He noted, "A second Aublet sheet at the British Museum may be an isolectotype but it has incomplete leaves. Neither sheet bears reproductive parts." Cowan offers further discussion on page 39. BM.

RONABEA LATIFOLIA (**1:** 154. *t. 59* (*Ronobea*))—NG, TS—Rubiaceae = **Psychotria erecta** (Aublet) Standley & Steyerm., not *P. latifolia* Humb. & Bonpl. The basionym is *Ronabea erecta* Aublet (**1:** 156; not illustrated). BM, P-R 8: 289.

ROPOUREA GUIANENSIS (**1:** 198. *t. 78* (*guyannensis*))—NG, TS—Ebenaceae = **Diospyros martinii** Benoist ex Amshoff, not *Diospyros guianensis* (Aublet) Gürcke. *Ropourea* Aublet is listed as a nomenclatural synonym and is rejected for the conserved *Idesia* Maxim. (#5331). It appears that *Idesia* Scopoli (1777) was illegitimate when published. P-R 8: 276.

ROUHAMON GUIANENSIS (**1:** 93. *t. 36* (*guyannensis*))—NG, TS—Loganiaceae = **Strychnos guianensis** (Aublet) Martius. In various publications on *Strychnos,* neither Monachino nor Krukoff has indicated a type specimen. Lanjouw and Uittien (1940, p. 157) suggested that P-R 4: 134 is not this species. P-A 7211 is a better match.

ROUPALA MONTANA (**1:** 83. *t. 32*)—NG, TS—Proteaceae = **Roupala montana** Aublet. BM, LINN-SM 157.1, P-R 3: 102.

ROUREA FRUTESCENS (**1:** 467. *t. 187*)—NG, TS—Connaraceae = **Rourea frutescens** Aublet. BM. Schellenberg's annotation on this sheet states that the type is at P.

RUELLIA RUBRA (**2:** 666. *t. 270*)—Acanthaceae = **Arrhostoxylum rubrum** (Aublet) Nees. BM.

RUELLIA VIOLACEA (**2:** 668. *t. 271*)—Acanthaceae = **Arrhostoxylum violaceum** (Aublet) Nees. Lemée (1953, p. 484) used "*D[ipteracanthus]*? *violaceus*." BM.

SABICEA ASPERA (**1:** 194. *t. 76*)—NG, TS—Rubiaceae = **Sabicea aspera** Aublet. This taxon was designated the lectotype species by Steyermark (Mem. New York Bot. Gard. **17**(1): 307. 1967). BM, LINN-SM 342.2, P-R 8: 274.

SABICEA CINEREA (**1:** 192. *t. 75*)—Rubiaceae = **Sabicea cinerea** Aublet. BM, P-R 8: 274.

SAGONEA PALUSTRIS (**1:** 285. *t. 111*)—NG, TS—Hydrophyllaceae = **Hydrolea palustris** (Aublet) Raeuschel. LINN-SM 469.3, P-R 11: 351.

SALVINIA AURICULATA (**2:** 969. *t. 367*)—Salviniaceae = **Salvinia auriculata** Aublet. No supporting specimen located.

SAOUARI GLABRA (**1:** 599. *t. 240*)—NG, TS—Caryocaraceae = **Caryocar glabrum** (Aublet) Pers. Prance (Fl. Neotrop. **12:** 40. 1973) designated a specimen at BM as the type. LINN-SM 968.3, P-J 11425B.

SAOUARI VILLOSA (**1:** 601. *t. 241*)—Caryocaraceae = **Caryocar villosum** (Aublet) Pers. BM, P-J 11426.

SAPINDUS ARBORESCENS (**1:** 357. *t. 139*)—Sapindaceae = **Matayba arborescens** (Aublet) Radlk. BM.

SAPINDUS FRUTESCENS (**1:** 355. *t. 138*)—Sapindaceae = **Pseudima frutescens** (Aublet) Radlk. A specimen at BM was photographed by Meyer (#3576) but was not located.

SAUVAGESIA ADIMA (**1:** 251. *t. 100, fig. a*)—Ochnaceae = **Sauvagesia erecta** L. P-R 6: 212.

SAUVAGESIA ERECTA (**1:** 254. *t. 100, fig. b*)—Ochnaceae = **Sauvagesia sprengelii** St. Hil. P-A 20653, P-R 6: 212.

SENAPEA GUIANENSIS (Suppl. 22. *t. 381*)—NG, TS.

Airy Shaw (*in* Willis, 1973, p. 1059), apparently following Hallier (1918, p. 23), referred this genus to *Passiflora* with a question mark. The name was considered neither by Killip in his monograph of the Passifloraceae nor by Lemée. Tillett, who is working on the genus *Dilkea* (which seemed a possibility), has examined a photocopy of the specimen (BM) and is convinced that it is not a member of the Passifloraceae. If the fruit can be located, an identification might be possible (pers. comm.).

SERAPIAS CARAVATA (**2:** 816. *t. 320*)—Orchidaceae = **Elleanthus caravata** (Aublet) Reichenb. f. No supporting specimen located.

SIMABA GUIANENSIS (**1:** 400. *t. 153* (*guyannensis*))—NG, TS—Simaroubaceae = **Simaba guianensis** Aublet. P-J 13010 is indicated as "ex herb. Candolle."

SIMAROUBA AMARA (**2:** 860. *tt. 331, 332*)—NG, TS—Simaroubaceae = **Simarouba amara** Aublet. *Simarouba* Aublet is a conserved generic name (#4111), with the type species *Simarouba amara* Aublet, although Jansen-Jacobs (*in* Stoffers & Lindeman, eds., Fl. Suriname **5:** 326. 1979) places this taxon in the synonymy of *Quassia simaruba* L. f. BM.

SIMIRA TINCTORIA (**1:** 170. *t. 65*)—NG, TS—Rubiaceae = **Simira tinctoria** Aublet. Bremekamp (Acta Bot. Neerl. **3:** 150–153. 1954) discussed this genus in detail but did not designate a type. BM, P-R 8: 267.

SINGANA GUIANENSIS (**1:** 574. *t. 230* (*guyannensis*))—NG, TS—Leguminosae. Airy Shaw (*in* Willis, 1973, p. 1069) stated "? Leguminosae (inc. sed.)," while Farr *et al.* (1979, p. 1617) have "Leguminosae, Papilionaceae," attributed to R. Cowan. BM.

SIPANEA PRATENSIS (**1:** 148. *t. 56*)—NG, TS—Rubiaceae = **Sipanea pratensis** Aublet. BM, P-R 8: 281.

SIPARUNA GUIANENSIS (**2:** 865. *t. 333* (*guyannensis*))—NG, TS—Monimiaceae = **Siparuna guianensis** Aublet. BM.

SLOANEA SINEMARIENSIS (**1:** 534. *t. 212*)—Elaeocarpaceae = **Sloanea sinemariensis** Aublet. BM, LINN-SM 928.4.

SOLANUM TEGORÉ (**1:** 212. *t. 84*)—Solanaceae = **Cyphomandra tegore** (Aublet) Sendt. ex Walp. Specimen at BM annotated "*Cyphomandra hartwegii* sp. coll. A. Childs in 1974."

SORAMIA GUIANENSIS (**1:** 552. *t. 219* (*guyannensis*))—NG, TS—Dilleniaceae = **Doliocarpus guianensis** (Aublet) Gilg. BM.

SOUROUBEA GUIANENSIS (**1:** 244. *t. 97* (*guyannensis*))—NG, TS—Marcgraviaceae = **Souroubea guianensis** Aublet. BM, P-R 3: 168.

SPERMACOCE ALATA (**1:** 60. *t. 22, fig. 7*)—Rubiaceae = **Borreria alata** (Aublet) DC. Work in press by F. R. Fosberg may clarify this and some of the following taxa. Recent work has suggested that *Borreria* is synonymous with *Spermacoce*. All of Aublet's taxa of *Spermacoce* require careful study of the actual specimens, for few confident conclusions can be drawn from the descriptions or illustrations. P-R 3: 118 annotated by Sandwith.

SPERMACOCE ASPERA (**1:** 59. *t. 22, fig. 6*)—Rubiaceae = **Mitracarpus hirtus** (L.) DC. Sandwith (1963, p. 260) commented on this taxon. P-R 3: 118 annotated by Sandwith.

SPERMACOCE CAERULESCENS (**1:** 57. *t. 19, fig. 2*)—Rubiaceae = **Borreria latifolia** (Aublet) Schum. P-R 3: 118 annotated by Sandwith.

SPERMACOCE HEXANGULARIS (**1:** 61. *t. 22, fig. 8*)—Rubiaceae. Lemée (1953, p. 569) called this taxon "*Spermacoce sexangularis* Aublet," citing *S. hexangularis* Aublet as a synonym. No supporting specimens located.

SPERMACOCE LATIFOLIA (**1:** 55. *t. 19, fig. 1*)—Rubiaceae = **Borreria latifolia** (Aublet) Schum. No supporting specimen located.

SPERMACOCE LONGI-FOLIA (**1:** 58. *t. 21*)—Rubiaceae = **Mitracarpus hirtus** (L.) DC. See Sandwith (1963, p. 260). P-R 3: 118 annotated by Sandwith.

SPERMACOCE PROSTRATA (**1:** 58. *t. 20, fig. 3*)—Rubiaceae = **Spermacoce prostrata** Aublet. Fosberg (pers. comm.) stated that the type is in the Delessert herbarium at G. P-R 3: 118.

SPERMACOCE RADICANS (**1:** 58. *t. 20, fig. 4*)—Rubiaceae = **Diodia** sp. nov. ? See Sandwith (1963, p. 260). P-R 3: 118.

TABERNAEMONTANA ECHINATA (**1:** 263. *t. 103*)—Apocynaceae.
Allorge (pers. comm.) has suggested that the foliage shown in *plate 103* is to be called *Peschira echinata* (Aublet) DC. (*Anacampta echinata* (Aublet) Markgr.), and the fruit (*figs. 7, 8*) *Stenosolen heterophyllus* (Vahl) Markgr. No specimens were seen.

TACHIA GUIANENSIS (**1:** 75. *t. 29* (*guyannensis*))—NG, TS—Gentianaceae = **Tachia guianensis** Aublet. Maguire and Weaver (Jour. Arnold Arb. **56:** 113. 1975) cited the type as "P (IDC 6213.11: I 7)." P-R 3: 115.

TACHIBOTA GUIANENSIS (**1:** 287. *t. 112* (*guyannensis*))—NG, TS—Chrysobalanaceae = **Hirtella racemosa** Lam., not *H. guyanensis* (Fritsch) Sandwith. Prance (Fl. Neotrop. **9:** 326. 1972) cited Aublet specimens at BM and P-R (11: 352) without designating a lectotype.

TACHIGALI PANICULATA (**1:** 372. *t. 143, fig. 1*)—NG, TS—Leguminosae = **Tachigali paniculata** Aublet. Although Meyer photographed a specimen at BM (#2297), it was not located.

TACHIGALI TRIGONA (**1:** 374. *t. 143, fig. 2*)—Leguminosae = **Tachigali paniculata** Aublet. BM, LINN-SM 737.1.

TALIGALEA CAMPESTRIS (**2:** 625. *t. 252*)—NG, TS—Verbenaceae = **Amasonia campestris** (Aublet) Moldenke. *Amasonia* L. f. is a conserved generic name (#7156), and *Taligalea* Aublet is rejected. BM.

TALISIA GUIANENSIS (**1:** 349. *t. 136* (*guyannensis*))—NG, TS—Sapindaceae = **Talisia guianensis** Aublet. BM.

TAMONEA GUIANENSIS (**1:** 441)—Melastomataceae = **Miconia mirabilis** (Aublet) L. O. Williams. The change in name in the text and apparently on the plates of some copies is discussed under *Fothergilla* (q.v.). BM.

TAMONEA SPICATA (**2:** 660. *t. 268*)—NG, TS—Verbenaceae = **Tamonea spicata** Aublet. BM, LINN-SM 55.1.

TAMPOA GUIANENSIS (Suppl. 35. *t. 388* (*guyannensis*))—NG, TS—Celastraceae. Albert C. Smith (1940, pp. 553, 554) stated, "This monotypic genus is certainly not related to *Salacia*, as indicated by Hallier (Meded. Herb. Rijks Leiden **35:** 24. 1918)." Lemée (1952, p. 311) recognized the genus, while Airy Shaw (*in* Willis, 1973, p. 1129) stated without question that the genus equaled *Salacia* L. BM.

TANIBOUCA GUIANENSIS (**1:** 448. *t. 178* (*guyannensis*))—NG, TS—Combretaceae = **Terminalia dichotoma** G. F. W. Meyer, not *T. guianensis* Eichler. BM.

TAONABO DENTATA (**1:** 569. *t. 227*)—NG, TS—Theaceae = **Ternstroemia dentata** (Aublet) Sw. BM.

TAONABO PUNCTATA (**1:** 571. *t. 228*)—Theaceae = **Ternstroemia punctata** (Aublet) Sw. BM.

TAPIRIRA GUIANENSIS (**1:** 470. *t. 188* (*guyannensis*))—NG, TS—Anacardiaceae = **Tapirira guianensis** Aublet. LINN-SM 829.1.

TAPOGOMEA ALBA (**1:** 164. *t. 62, fig. 4*)—Rubiaceae = **Psychotria ulviformis** Steyerm., not *P. alba* Ruiz & Pavon. BM.

TAPOGOMEA GLABRA (**1:** 165. *t. 63*)—Rubiaceae = **Psychotria blepharophylla** (Standley) Steyerm., not *P. glabra* (Turrill) Fosberg. BM, LINN-SM 340.5, P-R 8: 265.

TAPOGOMEA PURPUREA (**1:** 162. *t. 62, fig. 3*)—Rubiaceae = **Psychotria variegata** Steyerm., not *P. purpurea* Merr. & Perry. BM, P-R 8: 265.

TAPOGOMEA TOMENTOSA (**1:** 160. *t. 61*)—Rubiaceae = **Psychotria poeppigiana** Mueller-Arg., not *P. tomentosa* Hemsley. BM, LINN-SM 340.4, P-R 8: 265.

TAPOGOMEA VIOLACEA (**1:** 157. *t. 60*)—NG, TS—Rubiaceae = **Psychotria apoda** Steyerm., not *P. violacea* Aublet. The generic name *Cephaëlis* Sw. is conserved (#8411), with the type species (also conserved) *C. muscosa* (Jacq.) Sw.; *Tapogomea* Aublet is listed as rejected. Steyermark (*in* Maguire *et al.,* 1972, p. 406) has reduced *Cephaëlis* to a section of the genus *Psychotria.* LINN-SM 340.2, P-R 8: 265.

TAPURA GUIANENSIS (**1:** 126. *t. 48* (*guyannensis*))—NG, TS—Dichapetalaceae = **Tapura guianensis** Aublet. Prance (Fl. Neotrop. **10:** 68. 1972) cited specimens at BM and P but did not designate a lectotype. BM, P-R 6: 209.

TARALEA OPPOSITIFOLIA (**2:** 745. *t. 298*)—NG, TS—Leguminosae = **Dipteryx oppositifolia** (Aublet) Willd. *Dipteryx* Schreber is a conserved generic name (#3845), with the type species conserved as *Dipteryx odorata* (Aublet) Willd. (based on *Coumarouna odorata* Aublet); *Taralea* Aublet is rejected. BM.

TARIRI GUIANENSIS (Suppl. 37. *t. 390* (*guyannensis*))—NG, TS—Simaroubaceae = **Picramnia guianensis** (Aublet) Jansen-Jacobs. *Picramnia* Sw. is a conserved generic name (#4131), and *Tariri* Aublet is rejected. De Candolle (Prodr. **2:** 66. 1825) published the name "*P*[*icramnia*] ? *tariri* (Aubl.) DC." based on *Tariri guianensis* Aublet. It is, of course, illegitimate. Aublet noted that his specimen was sterile. There are specimens at BM and P that are sterile, but P-J 16001 resembles the plate and is clearly a *Picramnia.*

THOA URENS (**2:** 874. *t. 336*)—NG, TS—Gnetaceae = **Gnetum urens** (Aublet) Blume. Markgraf annotated an Aublet collection (BM) as *Gnetum paniculatum* Spruce, stating that it is not the plant figured by Aublet. This information is given (Bull. Jard. Bot. Buitenzorg, III. **10:** 455. 1930) with no citation of other Aublet material, suggesting that the plate is the type.

TIBOUCHINA ASPERA (**1:** 446. *t. 177*)—NG, TS—Melastomataceae = **Tibouchina aspera** Aublet. BM, LINN-SM 654.6.

TICOREA FOETIDA (**2:** 689. *t. 277*)—NG, TS—Rutaceae = **Ticorea foetida** Aublet. BM.

TIGAREA ASPERA (**2:** 918. *t. 350*)—NG, TS—Dilleniaceae = **Tetracera tigarea** DC., not *T. aspera* Raeuschel. Kubitzki (Mitt. Bot. Staatssam. München

9: 94. 1971) noted that, while *Davilla aspera* (Aublet) Benoist was based on *Tigarea aspera* Aublet, the specimen Benoist saw in the Lamarck herbarium was *Davilla kunthii* St.-Hil. The original *Tigarea aspera* specimen at BM is *Tetracera tigarea* DC., as was indicated by Kubitzki earlier (Mitt. Bot. Staatssam. München **8:** 67–69. 1970). Specimen at BM annotated "holotype" by Kubitzki.

TIGAREA DENTATA (**2:** 920. *t. 351*)—Dilleniaceae = **Doliocarpus dentatus** (Aublet) Standley. BM.

TOCOCA GUIANENSIS (**1:** 438. *t. 174* (*guyannensis*))—NG, TS—Melastomataceae = **Tococa guianensis** Aublet. LINN-SM 782.36, 782.37; P-J 14113.

TOCOYENA LONGIFLORA (**1:** 131. *t. 50*)—NG, TS—Rubiaceae = **Tocoyena longiflora** Aublet. BM, P-R 6: 200.

TONINA FLUVIATILIS (**2:** 857. *t. 330*)—NG, TS—Eriocaulaceae = **Tonina fluviatilis** Aublet. BM.

TONTANEA GUIANENSIS (**1:** 108. *t. 42* (*guyannensis*))—NG, TS—Rubiaceae = **Coccocypselum guianensis** (Aublet) Schum. P-J 9971, P-R 3: 128.

TONTELEA SCANDENS (**1:** 31. *t. 10*)—NG, TS—Celastraceae = **Tontelea scandens** Aublet. Albert C. Smith (1940, pp. 484, 485) recognized *Tontelea scandens* Aublet and cited for illustrations "Aubl. Pl. Guian. 3: *pl. 10* (exclu. *f. 10*). 1775." Such a figure is not numbered in the copies of Aublet I have had available for study. Smith (*Ibid.,* p. 484) stated, "It seems that Miers (20: 382) [Trans. Linn. Soc. 28: 382] is quite correct in taking Aublet's plate to be a mixture and also in interpreting the species as he does. The detached leaf was taken by Miers as his *Tontelea Aubletiana,* which I have elsewhere referred to *Cheiloclinium cognatum.* Aublet's description of the stamens as attached within a cupular disk and the style as short (not lacking) indicates that his flowers were not to be associated with the detached leaf but probably were correctly associated with the illustrated branchlet." Under *Cheiloclinium cognatum* (Miers) A. C. Sm., A. C. Smith (1940, p. 529) cited in synonymy *Tontelea aubletiana* Miers, Trans. Linn. Soc. **28:** 383. 1872, for the detached leaf of *Tontelea scandens* in Aublet *plate 10, figure 10.* Subsequently, Lemée (1952, p. 310) recognized *Salicia scandens* (Aublet) Griseb., unaware of the confusion of sheets with discordant elements. The specimen at BM, LINN-SM 87.1, and P-R 1: 54 represent the mixtures in this collection.

TOPOBEA PARASITICA (**1:** 476. *t. 189*)—NG, TS—Melastomataceae = **Topobea parasitica** Aublet. BM.

TOUCHIROA AROMATICA (**1:** 385. *t. 148*)—NG, TS—Leguminosae = **Crudia aromatica** (Aublet) Willd. *Crudia* Schreber is a conserved generic name (#3495), with the conserved type species *Crudia spicata* (Aublet) Willd. (based on *Apalatoa spicata* Aublet); *Touchiroa* Aublet is rejected. BM.

TOULICIA GUIANENSIS (**1:** 359. *t. 140* (*guyannensis*))—NG, TS—Sapindaceae = **Toulicia guianensis** Aublet. BM.

TOUNATEA GUIANENSIS (**1:** 550. *t. 218* (*guyannensis*))—NG, TS—Leguminosae = **Swartzia guianensis** (Aublet) Urban. *Swartzia* Schreber is a conserved generic name (#3574), and *Tounatea* Aublet is rejected. Richard Cowan (Fl. Neotrop. **1**: 144. 1968) discussed the typification of this taxon and concluded that an unnumbered Aublet collection at BM was the "isotype." BM, LINN-SM 958.4.

TOUROULIA GUIANENSIS (**1**: 492. *t. 194* (*guyannensis*))—NG, TS—Quiinaceae = **Touroulia guianensis** Aublet. No supporting specimen located.

TOVOMITA GUIANENSIS (**2**: 957. *t. 364* (*guyannensis*))—NG, TS—Guttiferae = **Tovomita guianensis** Aublet. Sandwith (1931, p. 176) discussed this taxon and referred to a specimen (BM), which was not located.

TRIFOLIUM GUIANENSE (**2**: 776. *t. 309* (*guyannense*))—Leguminosae = **Stylosanthes guianensis** (Aublet) Sw. In a monograph of the genus (Ann. Missouri Bot. Gard. **44**: 332. 1956), Mohlenbrock used "*guyanensis*"; he saw only a photo of an Aublet specimen. Specimen at BM annotated "lectotype" by t'Mannetja.

TRIGONIA LAEVIS (**1**: 390. *t. 150*)—Trigoniaceae = **Trigonia laevis** Aublet. BM.

TRIGONIA VILLOSA (**1**: 388. *t. 149*)—NG, TS—Trigoniaceae = **Trigonia villosa** Aublet. BM, P-J 12036.

TRIPLARIS AMERICANA (**2**: 910. *t. 347*)—Polygonaceae = **Triplaris surinamensis** Cham. (Brandbyge, pers. comm.). BM specimen may be on loan. LINN-SM 148.3.

TURNERA FRUTESCENS (**1**: 290. *t. 113, fig. 2*)—Turneraceae = **Turnera rupestris** Aublet var. **frutescens** (Aublet) Urban. Specimen at BM labeled holotype; LINN-SM 540.9; P-A 16418, 16419; P-R 11: 354.

TURNERA GUIANENSIS (**1**: 291. *t. 114* (*guyannensis*))—Turneraceae = **Turnera guianensis** Aublet. BM, LINN-SM 540.7, P-R 11: 354.

TURNERA RUPESTRIS (**1**: 289. *t. 113, fig. 1*)—Turneraceae = **Turnera rupestris** Aublet. Specimen at BM labeled "holotype"; LINN-SM 540.8.

VANTANEA GUIANENSIS (**1**: 572. *t. 229* (*guyannensis*))—NG, TS—Humiriaceae = **Vantanea guianensis** Aublet. BM.

VATAIREA GUIANENSIS (**2**: 755. *t. 302* (*guyannensis*))—NG, TS—Leguminosae = **Vatairea guianensis** Aublet. BM.

VIOLA HYBANTHUS (**2**: 811. *t. 319*)—Violaceae = **Corynostylis arborea** (L.) Blake. BM.

VIOLA ITOUBOU (**2**: 808. *t. 318*)—Violaceae = **Hybanthus calceolaria** (L.) Schulze. P-J 12796.

VIROLA SEBIFERA (**2**: 904. *t. 345*)—NG, TS—Myristicaceae = **Virola sebifera** Aublet. I can find no published comment on the several fruits illustrated with this species, which clearly represent other species or genera. Albert C. Smith (Brittonia **2**: 393. 1957) designated *figures 1–5* for this species. No supporting material located.

VOCHY GUIANENSIS (**1**: 18. *t. 6* (*guyannensis*))—NG, TS—Vochysiaceae = **Vochysia guianensis** Aublet. *Vochysia* Aublet is a generic name conserved (#4266) with the corrected spelling of Poiret in Lamarck and the type species indicated as *V. guianensis* Aublet. Stafleu (Rec. Trav. Bot. Néerl. **41:** 452. 1948) designated the specimen at BM as the type but cited "Herb. Linn." and a reference to Lanjouw and Uittien. BM and LINN-SM 15.1 are annotated "typi duplum." One Aublet specimen at P (P-J 14135) has been annotated as *V. speciosa* Warming by Stafleu.

VOTOMITA GUIANENSIS (**1:** 91. *t. 35* (*guyannensis*))—NG, TS—Melastomataceae = **Votomita guianensis** Aublet. For discussion of this taxon, see Morley (Bull. Torrey Bot. Club **90:** 1–16. 1963), who cited P-R 4: 139 as the holotype. BM.

VOUACAPOUA AMERICANA (Suppl. 9. *t. 373*)—NG, TS—Leguminosae = **Vouacapoua americana** Aublet. *Andira* Juss. is a conserved generic name (#3841), with the type species listed as "*A. racemosa* Lamarck ex Jaume Saint-Hilaire (Dict. Sci. Nat. **2:** 137. 1804)." The genus is credited to Jussieu (Gen. Pl. 363. 1789 sem. 2). In fact, Lamarck published the name *Andira racemosa* (Encycl. Méth. Bot. **1:** 171) in 1783. The monotypic *Vouacapoua* Aublet is incorrectly listed as a *nomen rejiciendum.* Baillon (Adansonia **9:** 206–212. *pl. 4.* 1868–70) discussed this taxon, as did Huber (Bol. Mus. Paraense Hist. Nat. **6:** 221–225. 1910), and Amshoff (*in* Pulle, 1939, **2**(2): 88) has recognized this genus and species. Lamarck (*loc. cit.*) expressed doubt when he listed *Vouacapoua* Aublet as a variety in his description of *A. racemosa.* Presumably it was this listing that suggested the conservation of *Andira.* Urban (Symb. Antill. **8:** 300. 1920) noted that the Aublet genus differs from *Andira* in having a dehiscent fruit. BM, P-J 15671.

VOUAPA BIFOLIA (**1:** 25. *t. 7*)—NG, TS—Leguminosae = **Macrolobium bifolium** (Aublet) Pers. *Macrolobium* Schreber is a conserved generic name (#3517), with the conserved type species *Macrolobium bifolium* (Aublet) Pers. See also *Outea* Aublet. Specimen at BM annotated "isotype" by R. Cowan; LINN-SM 77.2, P-R 1: 47.

VOUAPA SIMIRA (**1:** 27. *t. 8*)—Leguminosae.
Although *Vouapa* Aublet was a *nomen rejiciendum* with the conservation of *Macrolobium,* R. Cowan (Mem. New York Bot. Gard. **8:** 335, 336. 1953) saw an isotype at BM and concluded, "It represents no recognized species of *Macrolobium.*" He placed *Macrolobium simira* (Aublet) Gmelin in the synonymy of *Vouapa simira,* which is not placed. BM, P-R 1: 47.

VOUARANA GUIANENSIS (Suppl. 12. *t. 374* (*guyannensis*))—NG, TS—Sapindaceae = **Vouarana guianensis** Aublet. BM.

VOYARA MONTANA (Suppl. 26. *t. 383*)—NG, TS—Capparaceae = **Capparis montana** (Aublet) Lemée. Lemée (1955, p. 666) used "*Capparis montana*? (*Voyara* m. Aubl. selon H. Hallier dans Meded. Riks. Herb. Leiden XXXV, 1918, 23)." The combination in *Capparis* is credited to Lemée in *Index Kewensis* (Suppl. 13, p. 23. 1966); however, in Supplement 9, p. 298 (1938), the genus *Voyara* was referred to *Capparis.* BM.

VOYRIA CAERULEA (**1:** 211. *t. 83, fig. 2*)—Gentianaceae = **Voyria caerulea** Aublet. Maas (pers. comm.) indicated that the "type" is at P. P-R 8: 262.

VOYRIA ROSEA (**1:** 209. *t. 83, fig. 1*)—NG, TS—Gentianaceae = **Voyria rosea** Aublet. Maas (pers. comm.) indicated that the "type" is at P. P-R 8: 262.

Waria zeylanica (**1:** 605. *t. 243*)—Annonaceae = **Uvaria zeylanica** L. *Waria* Aublet is regarded as an orthographic variant of *Uvaria* L. Aublet cited "L. Sp. 756," which refers to the second edition of *Species Plantarum*. No supporting specimens were located.

Xiphidium coeruleum (**1:** 33. *t. 11*)—NG, TS—Haemodoraceae = **Xiphidium coeruleum** Aublet. No supporting specimens were located.

Xylopia frutescens (**1:** 602. *t. 242*)—Annonaceae = **Xylopia frutescens** Aublet. No supporting specimens were located.

Xyris americana (**1:** 40. *t. 14*)—Xyridaceae or Abolbodaceae = **Abolboda americana** (Aublet) Lanjouw. Specimen at BM annotated "type"; P-R 1: 53.

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ARNOLD ARBORETUM
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

THE GENERA OF BURMANNIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

CARROLL E. WOOD, JR.

BURMANNIACEAE Blume, Enum. Pl. Javae **1**: 27. 1827, nom. cons.

(BURMANNIA FAMILY)

Annual (or perennial), autotrophic, partly autotrophic, or achlorophyllous "saprophytic" herbs. Leaves alternate, simple, entire, exstipulate, mostly reduced to scales, the photosynthetic species leafy stemmed, with or without a basal rosette of small, linear leaves. Flowers perfect, regular (actinomorphic) [or zygomorphic or rarely 2-lipped]. Inflorescences mostly monochasia or dischasia, often reduced to a single terminal flower or condensed and headlike. Perianth petaloid, white or colored, of 2 whorls of 3 tepals united to form a tube, the 3 inner usually smaller than the outer in Burmannieae [or the 3 outer smaller, often almost lacking in Thismieae]; perianth tube cylindrical or 3-angled, often 3-winged [or 3- or 6-ribbed]. Anthers 3 and opposite the inner perianth lobes [or in *Haplothismia* and most Thismieae 6], sessile or subsessile in the perianth throat [or with short recurved filaments], 4-loculate, latrorse [or introrse], connective broad, often appendaged at top and/or base; pollen grains single or in tetrads [or dyads], 1- or 2-porate [4-porate or 1-colpate]. Gynoecium 3-carpellate, syncarpous; style single, filiform [or short-cylindrical or conical in Thismieae], tipped with 3 short branches, each with a single stigma [or with 3 sessile or connate stigmas]; ovary inferior, 3-locular with axile placentae or 1-locular with 3 parietal placentae [in some genera with a large, globose gland inside the ovary on each side of the top of each placenta!]; ovules numerous,

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[1] Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum currently made possible through the support of the National Science Foundation, under Grant DEB-81-11520 (Carroll E. Wood, Jr., and Norton G. Miller, principal investigators). This treatment, the 97th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area but with information about extra-regional members of a family or genus in brackets [ ]. References that I have not verified are marked with an asterisk.

I am indebted to my colleagues Norton G. Miller, George K. Rogers, and Barbara Nimblett for their help with various aspects of the work on this family; to Christopher S. Campbell for Kodachrome pictures and alcohol-preserved material of *Apteria* and of *Burmannia biflora*; and to Walter S. Judd for alcohol-preserved material of *Burmannia capitata* and fruits of *Apteria*. The illustration of *Apteria* was drawn by Margaret van Montfrans from my dissections of the specimens sent by Drs. Campbell and Judd.

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minute, anatropous, 2-integumented, tenuinucellar; female gametophyte of the Polygonum or the Allium type. Perianth persistent on the fruit [or the upper part bearing the stamens deciduous, only the lower part persistent, or in Thismieae the entire perianth circumscissile, leaving only a basal thickened ring]. Fruit capsular [sometimes fleshy in Thismieae], dehiscing irregularly or splitting transversely [or at the top] or sometimes by valves. Seeds numerous, small; embryo minute, undifferentiated, sometimes composed of only a few (3–6) cells; endosperm present, usually consisting of relatively few, large cells. (Including Thismiaceae J. G. Agardh, nom. cons.; excluding Corsiaceae Beccari, nom. cons.) TYPE GENUS: *Burmannia* L.

A small family of 17 or 18 genera and about 135 species of perennial or annual mycotrophic herbs, varying from leafy-stemmed, green autotrophs to scale-leaved, achlorophyllous "saprophytes." The family occurs primarily in the tropics and subtropics of North and South America, Africa, Asia, and Australia, but with extensions northward to Virginia and Illinois in the United States and to southern Japan, and southward to Brazil and Argentina; Angola, South Africa, and Madagascar; and southeastern Australia, Tasmania, and northern New Zealand. The distribution of *Burmannia* L. (*q.v.*) is nearly that of the family; *Gymnosiphon* Blume occurs in Central and South America, the West Indies, tropical Africa, Madagascar, Malaysia, Indonesia, and New Guinea; and *Thismia* occurs in the Americas, tropical Asia, and Australia–New Zealand. Twelve genera are indigenous in South America, and six of these extend into North America, with *Burmannia* L. and *Apteria* Nutt., of tribe Burmannieae, and *Thismia,* of tribe Thismieae, reaching the United States. Although most genera are confined to the Americas, to Africa, or to Asia-Australia, there are some truly extraordinary disjunctions. *Glaziocharis* Taub. ex Warm. has two species: *G. macahensis* Taub. ex Warm., known only from Rio de Janeiro, Brazil, and *G. Abei* Akasawa, known from Shikoku and southern Kyushu, Japan. *Thismia* Griff. sect. RODWAYA Schlechter includes only two closely related species: *T. Rodwayi* F. Mueller (*Bagnisia Hillii* Cheeseman), of Australia (eastern Victoria and Tasmania) and New Zealand (North Island), and *T. americana* N. E. Pfeiffer, known from only one colony discovered on low prairies near Chicago in 1912 and presumably now extinct. A more familiar pattern is seen in *Burmannia,* in which there are several tropical American–tropical Asian disjunctions.

The family is generally regarded as being composed of two or three groups of genera that have been ranked by various authors as tribes, subfamilies, or families (see Jonker, 1938; Lawrence). Bentham & Hooker, Baillon, and Engler, among others, considered the Burmanniaceae to consist of tribes Burmannieae (Euburmannieae), Thismieae, and Corsieae. Thorne recognized these same groups at the rank of subfamily, while Hutchinson treated them as distinct families. Jonker, Takhtajan, Cronquist, and others have maintained Corsiaceae and Burmanniaceae (with tribes Burmannieae and Thismieae) as distinct families. Airy Shaw established a new tribe, Haplothismieae, to accommodate *Haplothismia annulata* Airy Shaw (of South India) in Burmanniaceae, kept tribes Burmannieae and Thismieae, and maintained Corsiaceae as a separate family.

The Burmanniaceae have been placed variously in relation to other families of monocotyledons. They have often been associated with the Orchidaceae on the basis of their minute seeds that supposedly lack endosperm. Endosperm, although scant, does occur, however, and Jonker (1938, p. 6) wrote, "The presence of endosperm and the construction of the flower makes relationship with the *Liliiflorae* highly probable. Of this order *Amaryllidaceae, Iridaceae* and *Taccaceae* seem to be most closely related." Hutchinson (1973, p. 838) placed the Burmanniales (Burmanniaceae, Thismiaceae, Corsiaceae) "next to *Haemodorales,* and especially near *Hypoxidaceae* (*Curculigo*)." He remarked, however, that "the affinity with *Orchidaceae* is probably closer than at first appears, the two groups having developed on parallel lines with regard to certain characters such as saprophytism and minute seeds." At present, most authors seem to favor a position for Burmanniaceae in or near the Liliales, but Cronquist maintains the order Orchidales to include Orchidaceae, Geosiridaceae (removed from Burmanniaceae by Jonker), Burmanniaceae, and Corsiaceae. Melchior, Thorne, and Takhtajan all have favored Liliales (Liliiflorae), Melchior placing Burmanniaceae and Corsiaceae in suborder Burmanniineae and Thorne linking Burmanniaceae (with subfamilies Burmannioideae, Thismioideae, and Corsioideae) and Iridaceae (with subfamilies Iridoideae and Geosiridoideae) in suborder Iridineae. Takhtajan thinks the Burmanniaceae to be closely related to Liliales, especially Iridaceae, and evidently derived from them.

Many species of Burmanniaceae are known only from single collections or localities. As a result, although general morphology is the best-known feature of the group, the detailed morphology, mycorrhizal relationships, embryology, and palynology are known for only relatively few species, and the physiological ecology, floral biology, cytology, and chemistry are nearly untouched.

The species of *Burmannia,* the largest genus of the family, range from leafy, green autotrophs to achlorophyllous "saprophytes." The other members of the family appear to be achlorophyllous. Those plants that have been studied are endomycorrhizal, and it has long been assumed that the achlorophyllous Burmanniaceae, most of which "occur almost exclusively on decaying leaves, wood and roots in the deep shade of tropical, wet, primeval forests" (Jonker, 1938, p. 13) are saprophytes. However, in view of research on *Monotropa* (Ericaceae subfam. Monotropoideae) and Orchidaceae (see Furman & Trappe), it seems much more probable that these, along with similar achlorophyllous plants such as *Voyria* (*Leiphaimos*) (Gentianaceae) (see Wood & Weaver), *Sciaphila* (Triuridaceae), and *Epirrhizanthes* (Polygalaceae) that sometimes grow intermixed with them, are instead epiparasites that parasitize the roots of vascular plants, although not directly attached to them, via a shared mycorrhizal fungus. Jonker (1938, p. 12) remarked about *Thismia americana*: "It is hard to believe that Chicago is the normal area for this species, but I cannot give a satisfactory explanation why it occurs there. The habitat, an open prairie among the moss, is very different to the habitats of other *Thismias,* usually growing saprophytically in primeval forests." Epiparasitism of the *Monotropa* type makes such a habitat both quite possible and believable.

The family is of no economic importance.

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KEY TO THE GENERA OF BURMANNIACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Small, erect, green or purplish herbs with solitary or cymose flowers; perianth petaloid, regular, the tepals in 2 whorls of 3, united; anthers 3, nearly sessile on the perianth below the inner whorl of tepals, opening horizontally, the connective appendaged; gynoecium 3-carpellate, syncarpous, the ovary inferior; fruit a capsule topped* *by the persistent perianth; seeds numerous, minute, the embryo undifferentiated, the endosperm scanty.*

Ovary 3-locular, with axile placentae; flowers with or without wings; capsule opening by horizontal fissures or irregular splits; plants green, with or without a basal rosette of linear leaves and with small linear to lanceolate cauline leaves. . . . . . 1. *Burmannia.*

Ovary 1-locular, with 3 parietal placentae; flowers wingless; capsule opening from base by 3 upward-curling valves (see FIG. 1, k); plants without basal leaves, stem and scalelike leaves purplish or violet. . . . . 2. *Apteria.*

Tribe BURMANNIEAE

Subtribe **Burmanniinae**

1. **Burmannia** Linnaeus, Sp. Pl. 287. 1753; Gen. Pl. ed. 5. 139. 1754.

Erect, terrestrial [rarely pendent, epiphytic], annual [or perennial], autotrophic [or "saprophytic" (more probably epiparasitic)], mycorrhizal herbs. Stems 3–60 cm (ours usually less than 25 cm) tall, usually simple (sometimes branched) [in sect. FOLIOSA with conspicuous grasslike parallel-veined decurrent leaves to 25 cm long or] with variously reduced, often scalelike leaves and with or without a rosette or a few linear-lanceolate to linear or subulate leaves at the base. Flowers small (in ours 2–12 mm long), blue, pink, white, yellow, or greenish, erect [or rarely pendulous], winged or wingless, usually in the axil of a small bract, basically in bifid cymes (monochasia or dichasia) of 2 to 15 (to many) flowers, but by reduction solitary at the stem tip or in some (e.g., *B. capitata*) the cymes contracted into a head. Perianth with 6 small, erect [rarely spreading] lobes, these often with inrolled margins, the 3 outer lobes smaller than the 3 inner, the tube ± cylindrical, 3-angled or 3-winged. Anthers 3, nearly sessile on the perianth below the inner perianth lobes, the connective broadly triangular in ours, bearing the 4 locules at its margins and in most species with 2 apical appendages or crests at its apex and in some species (e.g., *B. flava*) also with a median appendage at the base; locules dehiscing horizontally; pollen grains single [or in dyads or tetrads], 1-porate, 1- or 2-porate, [or 2-porate]. Style filiform, divided into 3 short branches at the top, each branch with a funnel-shaped, bowl-shaped, or peltate stigma [or stigmas sessile at top of style]. Ovary 3-angled, with or without wings, 3-locular, the placentae axile, with numerous minute ovules. Perianth persistent and drying atop the winged or wingless capsule; capsule opening by irregular horizontal fissures. Seeds very numerous, minute, oblong to ellipsoid; embryo undifferentiated; endosperm scarce. (*Tripterella* Michaux) TYPE SPECIES: *B. disticha* L., $2n =$ ca. 136; effectively typified by Linnaeus (see below); see also Britton & Brown, Illus. Fl. No. U. S. & Canada. ed. 2. **1:** 547. 1913. (Name commemorating the Dutch botanist Johannes Burman, 1706–1779. Linnaeus wrote [in Critica Botanica, 1737; transl. Sir Arthur Hort, 1938], "*Burmannia* is a plant of Ceylon [Sri Lanka] with a double spike, seeing that Burman collaborated with Hermann in writing of the plants of that country.")

A genus of pantropical distribution with extensions into cooler areas in the southeastern United States (to southeastern Virginia and southeastern Oklahoma), southern Brazil (Rio Grande do Sul), Argentina (Corrientes), South Africa (Transvaal and Natal), Madagascar, southeastern Australia, and southern Japan (Honshu). Jonker (1938) recognized 57 species in two sections: FOLIOSA Jonker, including five perennial species with cauline, grasslike, parallel-veined leaves; and BURMANNIA, the remaining species, both chlorophyllous and achlorophyllous, with basal leaves (if present at all) reduced to a few linear leaves and stem leaves scalelike. With the exception of *Burmannia longifolia* Becc., which is widely distributed in Malaya, Indonesia, the Philippine Islands, and New Guinea, the members of sect. FOLIOSA are indigenous to the Western Hemisphere. Jonker recognized 12 species of sect. BURMANNIA in the Americas, 11 in Africa, and 30 in Asia and Australia. Subsequently, two species of sect. FOLIOSA (both leafy epiphytes) and three of sect. BURMANNIA have been described from South America.

Several of the species of *Burmannia* have very wide continental distributions, and Jonker has pointed out, in addition to the geographic disjunction in sect. FOLIOSA, close relationships between the West Indian–South American *B. bicolor* Martius, the African *B. latialata* Hua, and the Asiatic *B. coelestis* G. Don, $2n$ = ca. 32, which are hardly distinguishable, and between *B. tenella* Bentham, the only American achlorophyllous species, and *B. lutescens* Becc., of Malaya.

Three chlorophyllous species of sect. BURMANNIA occur in the southeastern United States. *Burmannia biflora* L., characterized by lack of a basal rosette of leaves and by small, bright blue to violet (to white), strongly three-winged flowers either solitary at the tip of the stem or in 1–15-flowered bifid cymes with a central terminal flower, is distributed sporadically in peaty bogs, in savannas, and on grassy pond shores from Collier County, Florida, northward on the Coastal Plain to southeastern Georgia, the Carolinas, and the southeasternmost counties in Virginia, and westward to western Florida, southern Alabama and Mississippi, northern Louisiana (Ouachita Parish), and southeastern Texas (Houston and Hardin counties).

The tropical American *Burmannia capitata* (J. F. Gmelin) Martius (*Tripterella capitata* Michaux), which has small cauline leaves and only a few basal leaves or none at all and small, pinkish, purple (rarely in our area), greenish, or nearly white, wingless flowers in contracted, terminal, headlike inflorescences, occurs in a variety of moist to wet acid habitats, including pinelands, seepage slopes, gravel pits, bogs, and pondshores from Lee and Highlands counties, Florida, northward to the central Piedmont of Georgia, and—on the Coastal Plain—to Lenoir and Harnett counties, North Carolina. It extends westward through Florida, southern Alabama, and southern Mississippi, to central Louisiana and eastern Texas (Smith, Robertson, and Gonzales counties), and it occurs disjunctly in southeastern Oklahoma (Pushmahata County). It is widely distributed southward through the West Indies and Central and South America: Cuba, Hispaniola, Puerto Rico, southern Mexico (Chiapas), Belize, Nicaragua, Panama, Colombia, Venezuela, Guyana, Surinam, French Guiana, Trinidad, Brazil, Bolivia, Paraguay, and Argentina (Corrientes).

Burmannia flava Martius, also of wide distribution, reaches the United States only in southern Florida, where it has been collected only twice (see Ward, 1979): near Fort Myers, Lee County, in 1916, and in the Fakahatchee Strand in central Collier County, in 1946. It occurs south of our area in Cuba, southern Mexico (Chiapas), Belize, Costa Rica, Colombia, Venezuela, Guyana, Surinam, Brazil, Bolivia, Paraguay, and Argentina (Misiones and Corrientes). It is characterized by linear-subulate rosulate and cauline leaves, and by greenish flowers with narrow yellow wings and yellow perianth lobes.

The anthers of all three species have two apical crests. Anthers of *Burmannia capitata* are unappendaged at the base, while those of *B. biflora* have a short, obtuse median appendage, and those of *B. flava* an acute, pendulous one.

At least *Burmannia biflora* has been found growing with *Apteria* in our area, and there are records of achlorophyllous species of *Burmannia* growing with other burmanniaceous genera (see Jonker, 1938, p. 13), but there seem to be no records of two species of *Burmannia* occurring together.

The wide range of ecophysiological types found in the genus—from leafy-stemmed autotrophic epiphytes, through reduced, scale-leaved but chlorophyllous, terrestrial types, to achlorophyllous "saprophytes"—merits investigation. The range within the single genus is perhaps comparable to that exemplified by the gentianaceous genera *Obolaria-Bartonia-Voyria* (see Wood & Weaver) or by the orchidaceous series *Listera-Goodyera-Myrmechis-Zeuxine* (*Z. purpurascens*)-*Corallorhiza* arranged by Montfort & Küsters (see Furman & Trappe). Although the mycorrhizae and the associated fungus have been described for several species of *Burmannia,* Van der Pijl's study of the endophytic fungus of *B. candida* Griff. ex J. D. Hooker, $2n = 12$, which he found to be a phycomycete, probably a member of the Peronosporaceae, appears to be the only attempt to identify the fungus associated with a species of *Burmannia* and to determine whether the same fungus is shared by different "saprophytes."

The floral biology and breeding system do not seem to have been investigated for any species of *Burmannia*; there are only a few recorded chromosome counts; and there seem to have been no investigations of the chemistry.

To judge from the limited liquid-preserved material available, it appears that the flowers of *Burmannia capitata* are self-pollinated, for the pollen seems to be shed before the flower bud opens, and the stigmas are covered with germinating grains. In *B. biflora* the small inner tepals are curved inward above the anthers, hiding them from sight, and the three stigmas protrude between the inner tepals. Whether or not our species actually are annuals is not well established.

Pollen of 19 species of *Burmannia* was studied by Chakrapani & Raj, who found that most species have one-porate grains, while *B. dasyantha* Martius has atreme grains, several species have one- *or* two-porate grains, and *B. congesta* (Wright) Jonker has two-porate grains. Pollen grains are single (or in tetrahedral tetrads [or dyads] in *B. aprica* (Malme) Jonker). Brewbaker found *Burmannia* to be one of only 10 genera (out of 1908) in which both two- and three-nucleate pollen have been more or less reliably reported. He confirmed the three-nucleate condition of pollen of *B. biflora,* but the two-nucleate pollen reported for *B. Championii* Thw., $2n = 12$, and *B. candida* should be reconfirmed. Both the Polygonum and the Allium types of megagametophyte development have been described in *Burmannia*. *Burmannia coelestis* is aposporous, with an unreduced megagametophyte. Embryos are rudimentary and undifferentiated (reportedly four-celled in *B. coelestis* and ten-celled in *B. capitata*). Endosperm ontogeny is A-form helobial in *B. coelestis* and *B. pusilla* (see Swamy & Krishnamurthy).

Burmannia appears to be most closely related to the South American genera *Campylosiphon* Bentham (*C. purpurascens* Bentham) and *Hexapterella* Urban (*H. gentianoides* Urban).

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Subtribe **Apteriinae** Jonker

2. **Apteria** Nuttall, Jour. Acad. Nat. Sci. Philadelphia 7: 64. *pl. 9, fig. 2.* 1834.

Small, erect, presumably annual mycotrophic herbs lacking chlorophyll. Roots short and thin. Stem simple (sometimes branched above), violet to purple, with 1 to few (to ca. 6, rarely to 10) flowers. Leaves small, scalelike, sessile. Flowers about 1[–2] cm long, the perianth blue, violet, or purplish, rarely white [or blue and white], narrowly campanulate [or salver or funnel shaped]; perianth lobes 6, all the same length, the outer ovate, the inner much narrower, the united part of the perianth more than 3 times the length of the lobes. Stamens adnate to perianth tube below the 3 inner segments, each subtended by a broadly V-shaped, almost saclike, vasculated ridge (cf. Figure 1, d–f); filament short and thick, bearing on the abaxial side a large, 2-lobed wing and at the top expanded into a broad horizontal connective; locules borne horizontally and opening latrorsely, exposing the large pollen grains (in tetrads) in 2 masses. Ovary ovoid, abruptly tapering into the filiform style which is expanded into 3 short branches at the top, each branch terminated by a dish-shaped stigma at the level of 2 of the anther locules of 2 adjacent stamens; ovary 1-locular with 3 large parietal placentae bearing numerous minute ovules. Capsule crowned by the persistent perianth, opening from the base by 3 upward-curling valves, the placentae persistent. Seeds minute, very numerous, ± ellipsoid; embryo undifferentiated; endosperm consisting of 50–80 large cells. Type species: *A. setacea* Nutt., nomen superfluum = *A. aphylla* (Nutt.) Barnh. ex J. K. Small (*Lobelia aphylla* Nutt., 1822). (Name from Greek, *a,* without, and *pteron,* wing—wingless, in contrast with the three-winged flower of *Burmannia bicolor* L., which Nuttall knew as *Tripterella caerulea* Ell.) — NODDING NIXIE (see J. K. Small, Man. SE. Flora, 1933), a vernacular name of unknown origin, possibly coined, but not very appropriate since the flowers seldom nod.

Three closely related species of the warmer parts of the Western Hemisphere: *A. aphylla,* which ranges from the southern United States to Brazil and Bolivia; *A. lilacina* Miers, known from Colombia, Brazil, and Argentina; and *A. gentianoides* Jonker, of Brazil, Paraguay, and Bolivia. The three differ in the shape and size of the perianth and in the structure of the stamens. Our single species, *A. aphylla* (*A. setacea* Nutt., *A. boliviana* Rusby, *A. hymenanthera* Miquel, *A. Ulei* Schlechter), is distributed from northeastern Florida and southwestern Georgia, westward through southern Alabama, Mississippi, and Louisiana, to southeastern Texas, and southward through Florida to Cuba, Hispaniola, Puerto Rico, Jamaica, Dominica, Guadeloupe, and Trinidad, as well as from Mexico and Belize southward through Costa Rica and Panama to Colombia, the Guinas, and Brazil and Bolivia. Jonker reduced *A. hymenanthera* to *A. aphylla* var. *hymenanthera* (Miquel) Jonker but noted that "intermediate forms occur between the species and its variety especially in the West-Indian Islands." Other workers may well decide on still further reduction.

A confusion that began with Nuttall himself is shown in Jonker's distribution map (1938, p. 37), which shows *Apteria aphylla* as occurring northward in the Mississippi Embayment past St. Louis, Missouri, and in the citation of four collections from the coast of Mississippi (p. 205) as being from Missouri. Nuttall (1834, p. 65) wrote, "Found in the vicinity of St. Louis, Missouri, by Mr. L. C. Beck; in Alabama by Doctor Gates; and discovered in East Florida by Mr. Ware, probably on the margins of shallow grassy ponds, the situations mostly affected by the Tripterellas." Whether or not Nuttall confused "St. Louis" with either Bay St. Louis or St. Louis Bay on the coast of Mississippi, or whether a label mistake was involved, *Apteria* occurs only in the southernmost parts of both Mississippi and Louisiana and is not known northward in either Arkansas or Missouri.

Little seems to be recorded about the biology of any of the species of *Apteria.* All are presumed to be annuals and saprophytes via their mycorrhizal association, although the habitats of at least *A. aphylla* (acid, swampy woods, at the edges of bogs and hammocks, and in pine flatwoods, often in the company of *Burmannia*) do not seem to be favorable for a saprophyte. It seems more likely that these are epiparasites (via their mycorrhizae) of the *Galeola* (Orchidaceae) or *Monotropa* (Ericaceae) type. Uphof, who studied *A. aphylla* at Orlando, Florida, did not observe insect visitors to the flowers, and on the basis of the presence in the flowers of pollen-eating mites covered with pollen and crawling over the stigmas, the position of the stigmas (between the pollen masses of adjacent anthers), and the apparent adnation of anther, pollen, and stigma, concluded that the flowers are mostly self pollinated. The essentially smooth pollen is borne in tetrahedral tetrads ca. 47 μm in diameter (Chakrapani & Raj) and is three-nucleate at the time it is shed (Brewbaker). The megagametophyte is of the Polygonum type. The embryo is only four-celled at the time the seed is shed.

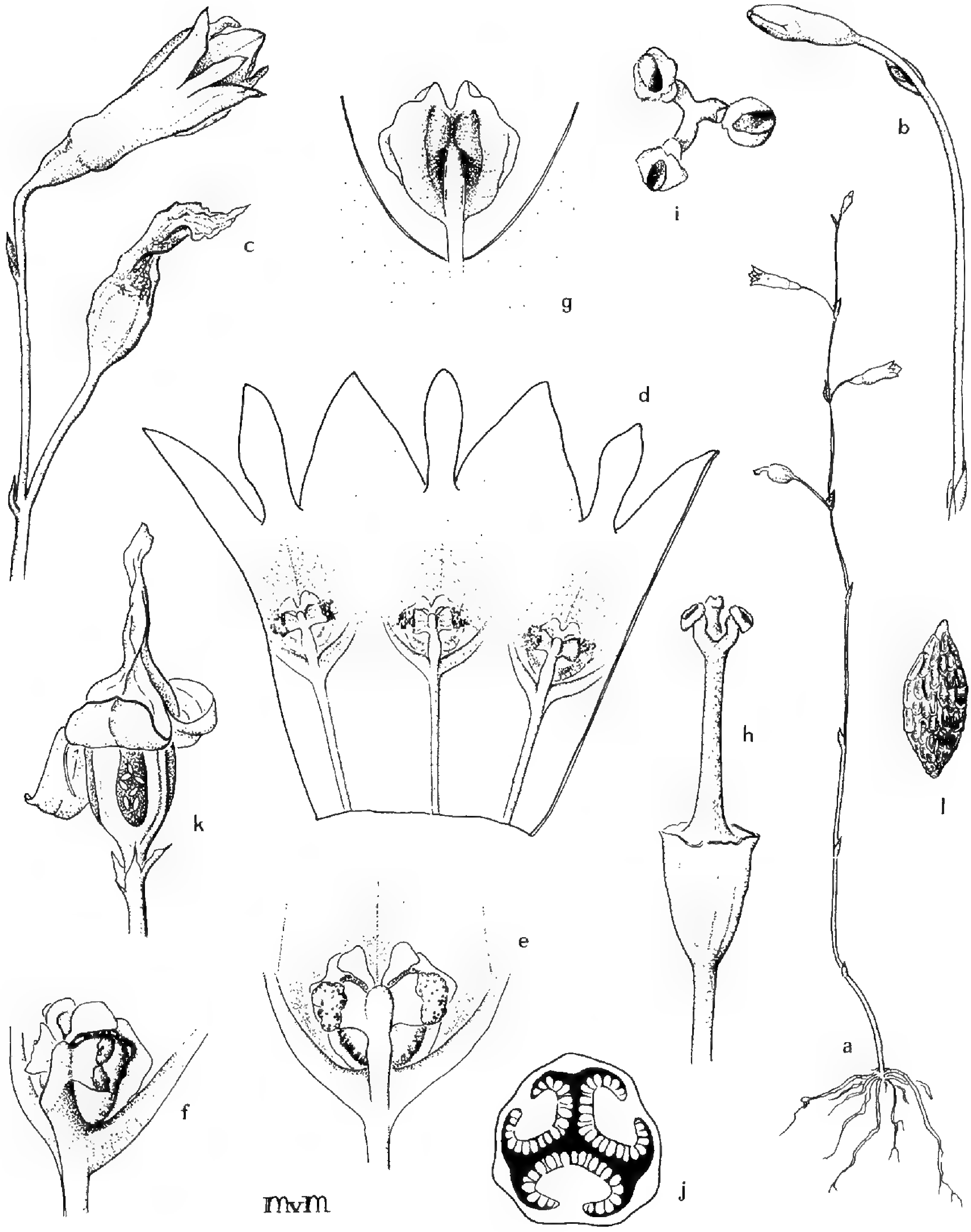

FIGURE 1. **Apteria.** a–l, *A. aphylla:* a, plant with immature fruit, two flowers at anthesis, and flower bud, × ¾; b, flower bud, × 3; c, flower and immature fruit with persistent perianth, × 3; d, perianth laid open to show stamens adnate to perianth, each stamen subtended by a V-shaped, saclike ridge, × 6; e, stamen, adaxial side, with adjoining parts of perianth, showing broad horizontal connective with masses of pollen tetrads at both sides and two-lobed, winglike appendage of filament behind, edges of wing inrolled, apex of wing lobes folded toward sides, × 12; f, same, oblique view, pollen removed to show two of four anther locules, × 12; g, stamen, abaxial side, showing two-lobed, winglike appendage of filament, anther connective and locules invisible behind it, perianth partially cut away to expose stamen, × 12; h, gynoecium, perianth cut away from top of ovary, × 6; i, stigmas and style branches from above, × 12; j, diagrammatic cross section of ovary to show placentation, × 12; k, capsule crowned by persistent perianth, three valves splitting away from placentae and curling upward, a few seeds persistent on placentae, × 6; l, seed, × 50.

The mature fruits are almost never collected and are little known. They should be looked for in localities where the plants have been found in flower. The capsule opens by three upward-curling valves, and the three placentae are persistent as shown in FIGURE 1, k.

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ARNOLD ARBORETUM
HARVARD UNIVERSITY
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

STUDIES IN MALESIAN PANDANACEAE, 19. NEW SPECIES OF FREYCINETIA AND PANDANUS FROM MALESIA AND SOUTHEAST ASIA

BENJAMIN C. STONE

DURING A STUDY VISIT of several months in the Harvard University Herbaria made possible through the courtesy of the Director of the Arnold Arboretum, several new taxa of *Freycinetia* and *Pandanus* were recognized. Their descriptions, presented here, form a part of the background necessary for the treatment of the Pandanaceae in *Flora Malesiana,* which is in preparation. I am grateful to the curators of the various herbaria listed herein for making these materials available for study.

Freycinetia Gaudich.

Sect. BLUMEELLA Stone

Freycinetia impudens B. C. Stone, sp. nov.

Liana modice robusta caulis foliosis usque ad 15 mm diametro. Folia coriacea usque ad 60–90 × 2.5–4 cm, lineari-lanceolata, sensim attenuato-acuminata, marginibus in basi breve tractu spinuloso-denticulatis, et apicem versus manifeste denticulatis (denticulis vix 1 mm longis, acicularibus, 2–5 mm sese separatis); costa media infra breviter carinato, basi inerme, apicem versus spinuloso-denticulata; pagina adaxiale minute obscureque striatula, abaxiale crebre venoso-striatula et subevidenter tessellata, reticulationibus ca. 2–3 × 0.4 mm, minutissime per stomata punctulatis; auriculis 7–12 × 8–11 cm, subrigide membranaceis, in sicco pallide brunneis, apice incurvato-subtruncatis, deinde persparse ciliato-denticulatis, margine integris. Inflorescentia terminalis, plerumque ternata; bracteis exterioribus foliaceis usque ad 35 cm longis, basi coloratis, carnosis, expansis; bracteis interioribus naviculari-deltoideis apice abrupte angustato-foliaceis, usque ad 15 cm longis, basi ca. 8 cm lato. Cephalia cylindracea, pedunculis usque ad 5 cm longis et 6 mm diametro, glabris (vel distaliter sparse minuteque hispidulis); cephalia immatura ca. 6–8 × 16 mm, carpidiis plerumque 2–4-natis, ca. 5 × 1 mm, pileo probabiliter 2.5 mm longo, vertice truncato, stigmatibus 2–4(–6) confluentibus, annulo angusto cincto. Spadix masculus ca. 12 cm longus, pedunculo glabro 5–7 cm longo et ca. 5 mm diametro, parte florifero ca. 7 cm longo et usque ad 9 mm diametro, staminibus congestis ca. 2–2.5 mm longis, filamentis 1.5–2 mm longis, antheris breve-oblongis ca. 0.8–1 mm longis obtusis. Cephalium bisexuale in specimine singulo (*Docters van Leeuwen 9986*) visum: carpidia et stamina intermixta,

Journal of the Arnold Arboretum **64**: 309–324. April, 1983.

filamentis staminorum 3.5–4 mm longis, antheris ut videtur normalibus, staminibus carpidium aequantibus vel leviter superantibus.

TYPE. New Guinea, Papua, Fly River 30 mi above D'Albertis junction, Oroville Camp, in rainforest, Aug. 1936, *L. J. Brass 7426* (holotype, A!).

ADDITIONAL SPECIMENS EXAMINED. **New Guinea.** IRIAN BARAT: Rouffaer R., 175 m alt., forested hills, *W. M. Docters van Leeuwen 9986* (BO!, L!); between Hollandia and Hollandia-Binnen, 80 m alt., secondary forest, *BW 3612, C. Kalkman* (L!).

Brass 7426 is one of the two specimens tentatively identified by Merrill and Perry as *Freycinetia pseudo-insignis* Warb. They remarked (J. Arnold Arb. **20:** 158. 1939): "Somewhat hesitantly we add here the following collection: *Brass 7426*. . . . This differs from the other collections in its obviously narrower leaves. The anthers of the ♂ inflorescence are about 3 mm. long [*sic*]." Martelli and Merrill and Perry have all mingled two species under the name *F. pseudo-insignis*; at least one of them (that now named above as *F. impudens*) and possibly the other cannot be equated with Warburg's species. Warburg's protolog calls for staminate spadices 8 cm long, the floriferous part 4 cm by 7 mm, and filaments 1.5 mm long. In *F. impudens* the spadices are about this size but the stamens are longer. Another very similar species is *F. inouei* Kanehira, also described from Irian Barat. Merrill and Perry thought this species to be the same as their *F. archboldiana,* and the two do belong together in Sect. BLUMEELLA. However, since the inflorescence in *F. inouei* appears to be regularly ternate (rather than multicephalic, as is the norm in *F. archboldiana*), it seems better to keep them distinct. On the other hand, it is possible that *F. inouei,* which was typified by a pistillate specimen, is the same taxon as *F. pseudo-insignis,* which was typified by a staminate one. In any case, *F. inouei* differs from *F. impudens* by its somewhat narrower and shorter leaves with less acuminate apices, smaller leaf prickles, and shorter, narrower spadices. The berries of *F. inouei* are mostly bistigmatic, while those of *F. impudens* are more frequently 3- to 5-stigmatic.

It is interesting to note the occurrence of bisexual cephalia in this species, a phenomenon rarely seen but known to date in *Freycinetia imbricata* Blume (*Bünnemeijer 5031,* from Sumatra), *F. negrosensis* Merr. (*Stone 12911,* from the Philippines), *F. scabripes* Warb. (*PNH 117425, Gutierrez et al.,* from the Philippines), and *F. reineckei* Warb. (*P. A. Cox,* several collections from Samoa). Only in the case of *F. reineckei,* however, is it known that both the male and the female organs in the cephalium are functional. Cox (pers. comm.) suggests that such bisexuality is an adaptive response to promote fertilization through bat pollination, since the bats are more attracted to polliniferous than to pistillate cephalia.

Sect. DEVRIESEELLA Stone

Freycinetia micrura B. C. Stone, sp. nov. FIGURE 1.

Liana habitu valde similis Freycinetia sphaerocephalo Gaudich. sed pedunculo foemineo densiter hispidulo, foliis parce angustioribus differt. Folia parva 7–10 cm × 4–7 mm, anguste elliptico-suboblanceolata, apice basinque angustata, apice sensim attenuato-caudato in caudo ca. 15–20 mm longo desinentio;

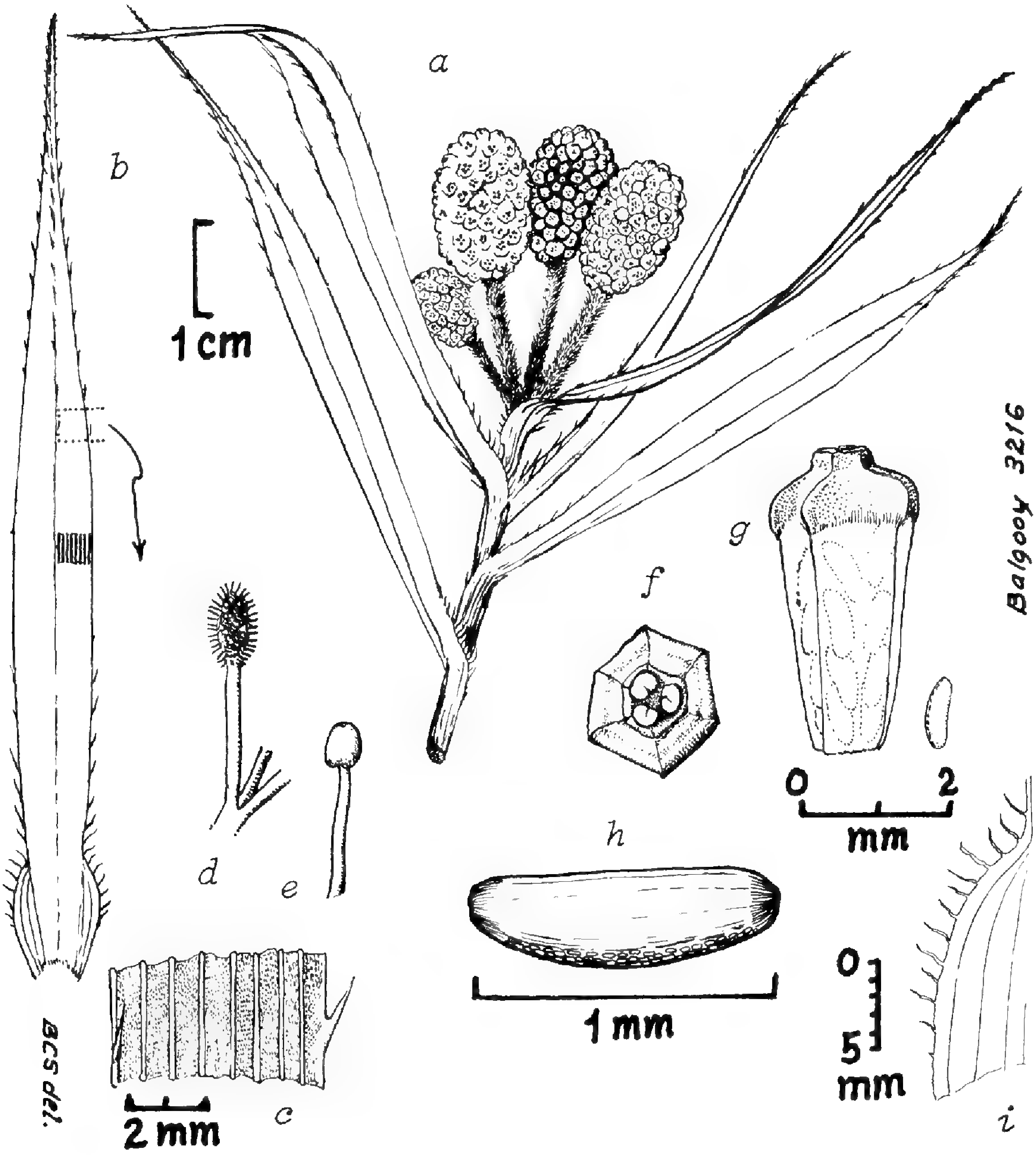


FIGURE 1. **Freycinetia micrura** (from *Van Balgooy 3216,* type collection): a, habit of fruiting branchlet; b, leaf, abaxial surface; c, portion of leaf margin, showing veins and marginal prickle; d, staminate spike; e, stamen, enlarged; f, berry, top view, showing 3 stigmas; g, berry, side view, seed beside it; h, seed, enlarged; i, auricle of leaf base, showing spinular margin.

vagina appresso, auriculis 12–14 × 2–3 mm, apice curvatis, marginibus spinuloso-pectinatis, spinulis angustis subrectis 0.8–1.8(–2) mm longis; lamina foliorum marginibus basi apiceque spinulosis (parte medio tertio inerme) vel, in foliis parvioribus, e basi ad apicem spinulosis; spinulis antrorsis vulgo 1 mm longis, apicem versus brevioribus (ca. 0.5 mm longis); costa media in parte dimidia distali spinulosis, spinulis ad eos in margine adjacentio similis, vulgo 1–2 mm sese separatis. Inflorescentia terminalis, ternata (vel quaternata), bracteis late ovatis, usque ad 30 × 15 mm, plus minusve caudatis, marginibus minute serrulato-spinulosis; pedunculo foemineo usque ad 20 mm longo, 2–

2.5 mm crasso, subcompresso, densiter hispidulo e basi ad apicem spinulis subappressis congestis 0.5 mm longis; cephalio ellipsoideo-subgloboso (ubi immaturo ca. 17 × 10 mm); gynoecio breve 4–5 × 1.5–2 mm, apice ca. 1 mm alto, late pyramidato-rotundato, areola centrali bi- vel quinque-stigmatifero ca. 1–1.4 mm lato instructo; seminibus immaturis ca. 1 mm longis. Cephalia mascula ca. 8–9 mm longae, pedunculo masculo laevi, glabro, ca. 15 mm longo; staminibus vix numerosis, filamentis 1.75 mm longis, antheris subgloboso-oblongis ca. 0.5 mm longis.

TYPE. Sulawesi, Mt. Roroka Timbu, western slope at 2000 m alt., in montane forest dominated by *Agathis* 40 m tall; climber with green fruit, bracts white, purple tipped; May 1979, *M. J. van Balgooy 3216* (holotype, L!).

A very distinct little plant evidently related to *Freycinetia sphaerocephala* Gaudich. of the Philippines, but differing markedly in the very densely hispidulous peduncles of the pistillate cephalia, and in the narrower leaves; the spinules of the leaf and auricle margins may be up to 2 mm long. The fruit described is unfortunately not yet mature.

I am grateful to Dr. van Balgooy for his kindness in allowing me to study the materials he collected, in advance of their distribution.

Pandanus L. ex Stickman

Sect. ACROSTIGMA Kurz

Pandanus ketele B. C. Stone, sp. nov. FIGURE 2.

Frutex gracilis, stipite erecto usque ad 3 m alto, 2–5 cm diametro, laevi, radicibus aereis basalibus, parvis, brevibus. Folia ca. 160 × 3.7–4.1 cm elongato-linearia, apice acutata, supra nitidam viridem, infra subglaucam, nervis longitudinalibus ca. 100 per foliam congestis; marginibus in basi (parte vaginanti ca. 7 cm longo excepto) spinuloso-denticulatis, denticulis patento-antrorsis curvatis usque ad 2 mm longis, 2–6 mm sese separatis, in medio, denticulis appressiter antrorsis, ca. 0.5 mm longis, 2–4 mm sese separatis, apicem versus, denticulis ca. 0.2 mm longis, ca. 1 mm sese separatis; costa media infra in basi denticulis unguiculiformibus usque ad 3 mm longis et 5–9 mm sese separatis, in medio denticulis parvis vel costa inerme carinata, deinde denticulis parvis vix 0.4 mm longis, 5–15 mm sese separatis, apicem versus denticulis parvissimis vix 0.2 mm longis, ca. 1 mm sese separatis; plicis binis apicaliventralibus in parte distale ca. 30 cm longo denticulatis, denticulis antrorsis parvis subirregulariter dispersis. Inflorescentia lateralis, gracilis, suberecta, ca. 64 cm longa, 14 mm diametro, parte distali fertili ca. 12 cm longo, capitulis congestis vulgo 7 aggregatis, parvis, ovato-subglobosis, subplano-convexis, 3.5–4.5 cm longis, subequidiametralibus, aurantiaco-rubris, e pluribus drupis compositis. Drupa ca. 2 cm longa (stylo incluso), pileo ca. 8 mm longo, 3 mm crasso, subacuto, in stylo spiniformi antrorse curvato 5–6 mm longo producto; parte seminifero ca. 8 mm longo.

TYPE. Papua New Guinea, Southern Highlands Province, Tari valley, Itipu village, ca. 1640 m alt., in swampy areas with secondary growth, Sept. 1981, *B. C. Stone & C. Rose 15005* (holotype, KLU!).

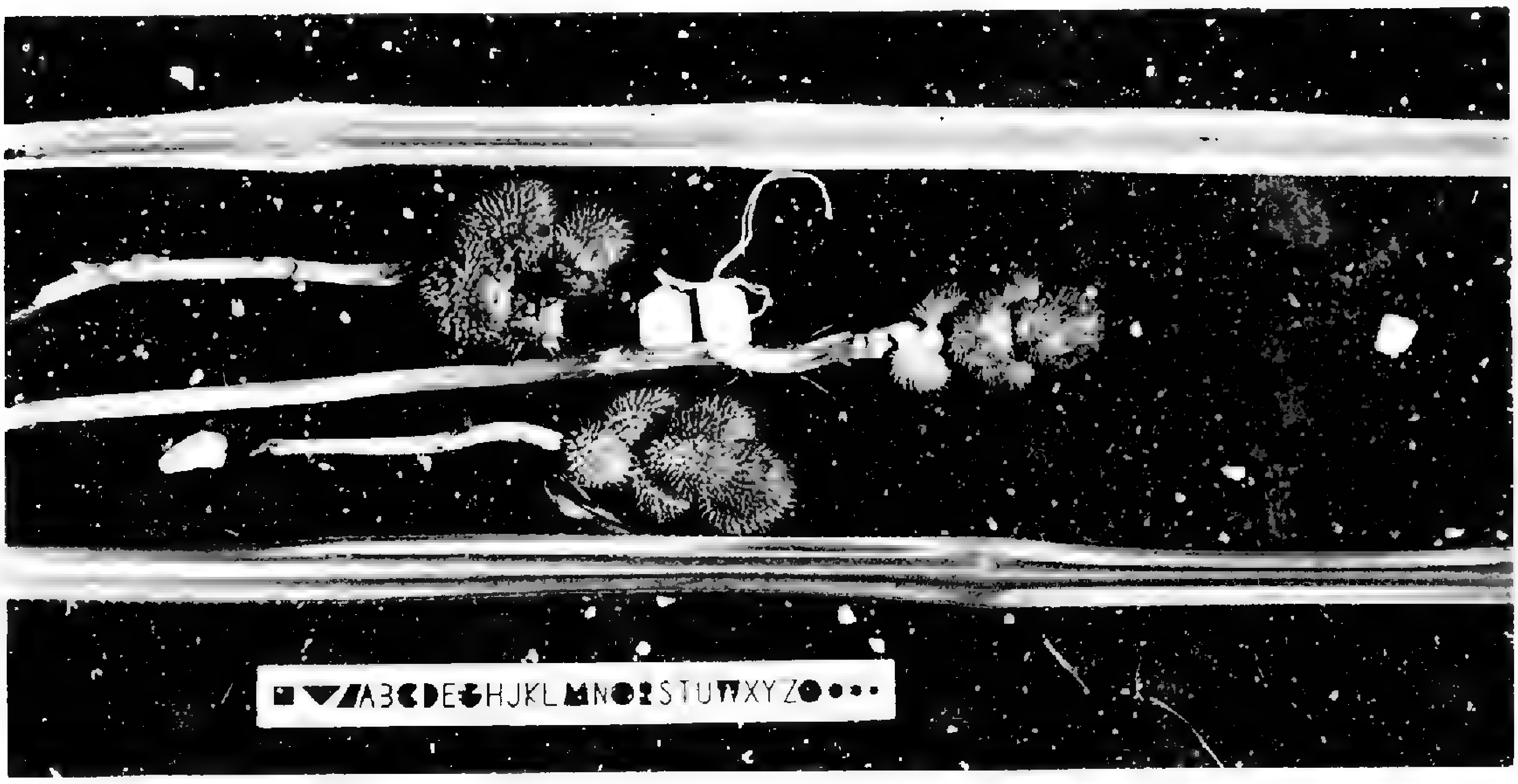


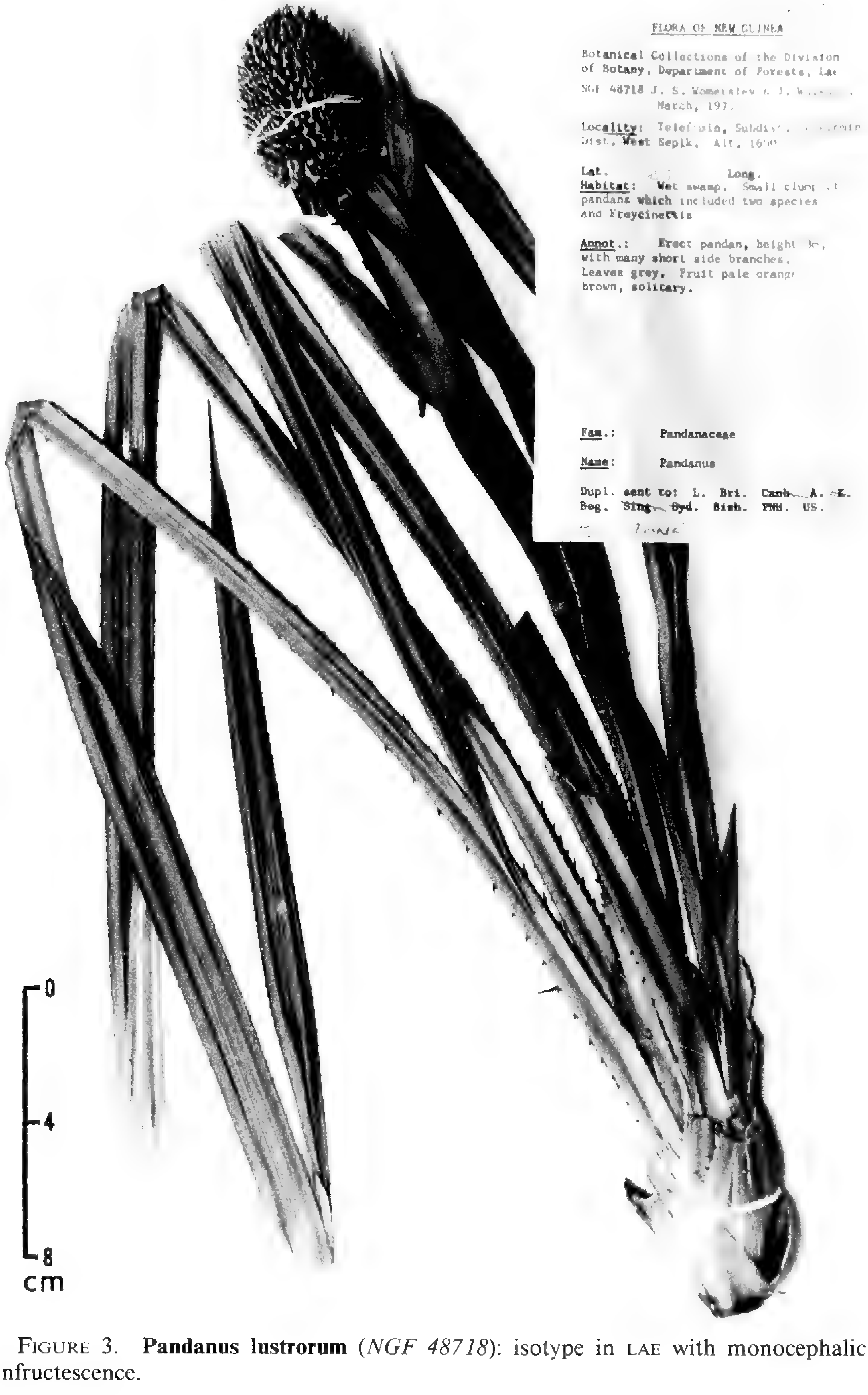
Figure 2. **Pandanus ketele:** leaves and infructescences of *Stone & Rose 15005* (type collection) photographed in the field. Ruler is 30 cm long.

This species clearly belongs with *Pandanus adinobotrys* Merr. & Perry, *P. setistylus* Warb., *P. angiensis* Kanehira, and *P. pseudosyncarpus* Kanehira, all of New Guinea (including Irian Barat), but differs from all of them in its much narrower leaves and its very long pistillate peduncle bearing small, crowded cephalia. Like these species it is characterized by lateral inflorescences—i.e., axillary fertile shoots that bear scale leaves (and occasionally some reduced foliage leaves) and floral bracts—that are clearly differentiated in function from the strictly foliage-bearing leaf crowns. All these species occur in the interior and mainly at intermediate altitudes, usually between 600 and 1800 m. *Pandanus ketele* occurs in small swamps and is sometimes cultivated as a hedge plant. The ripe drupes are dull vermilion, as is true for most (perhaps all) of the above-mentioned related species.

The collectors thank the children of Itipu village for help in collecting the material.

Pandanus lustrorum B. C. Stone, sp. nov. Figure 3.

Frutex erectus, stipite usque ad 4 m alto, ramis fertilibus lateralibus brevissimis, foliaceis. Folia anguste lineares acutissima usque ad 107 × 2 cm, in ramis fertilibus breviora, rigide coriacea, basi in vaginam brevem expansa; vagini ca. 2.5 cm longo striatulo-venoso; laminis obscure longitudinaliter venosis; marginibus in basi dentibus patenti-antrorsis ca. 2 mm longis, 1.5–8 mm sese separatis, in medio dentibus valde appressis vel antrorsis 0.6–1 mm longis, 4–8 mm sese separatis, apicem versus denticulis 0.4–0.7 mm longis, 0.5–0.9 mm sese separatis; costa media infra in basi dentibus reflexis usque ad 4 mm longis, 3–9 mm sese separatis, in medio denticulis antrorsis vix 1 mm longis, 3–10 mm sese separatis, apicem versus denticulis brevioribus denticulis marginorum similibus; plicis binis apicalibus denticulatis. Inflorescentia terminalis, pedunculo 30–35 cm longo, 5–6 mm diametro (in sicco), bracteato, distaliter infra cephalia modice sinuato; bracteis non vidi, delapsis. Cephalium ovoideum, 5.2



FLORA OF NEW GUINEA

Botanical Collections of the Division of Botany, Department of Forests, Lae

NGF 48718 J. S. Womersley & J. W[illegible] March, 197[illegible]

Locality: Telefomin, Subdist. [illegible] Dist., West Sepik. Alt. 1600

Lat. Long.

Habitat: Wet swamp. Small clump of pandans which included two species and Freycinetia

Annot.: Erect pandan, height 3m, with many short side branches. Leaves grey. Fruit pale orange brown, solitary.

Fam.: Pandanaceae

Name: Pandanus

Dupl. sent to: L. Bri. Cant. A. K.
Bog. Sing. Syd. Bish. PNH. US.

FIGURE 3. **Pandanus lustrorum** (*NGF 48718*): isotype in LAE with monocephalic infructescence.

× 4.8 cm, ca. 600 ad 800 drupis compositum, aurantiaco-brunneum; drupis angustis subfusiformibus, 13–19 mm longis (stylo incluso), parte basilari 6–8(–9) mm longo, pileo acutissime conico-pyramidato 5–7 mm longo apice in stylo antrorse deflecto spiniformi 4 mm longo producto. Mesocarpium superum medulloso-fibrosum, inferum fibrosum brevissimum. Endocarpium ca. 7 mm longum in parte dimidio basali situatum anguste obconicum, pariete ca. 0.15 mm crasso. Cetera ignota.

TYPE. Papua New Guinea, West Sepik Province, Telefomin, 1600 m alt., erect pandan in wet swamp, March 1975, *NGF 48718, Womersley & Waikabu* (holotype, KLU!; isotypes, BRI, L, LAE).

ADDITIONAL SPECIMENS EXAMINED. **New Guinea.** PAPUA NEW GUINEA. West Sepik Province: Telefomin, 1600 m alt., wet swamp, *NGF 48716, Womersley & Waikabu* (KLU, LAE), *NGF 20829, Henty* (LAE!).

This species is very much like *Pandanus adinobotrys,* and previously the above-mentioned specimens were assigned to that species. However, the specimens differ in their narrower leaves, often solitary fruit-head, and shorter styles, and they therefore appear to represent a somewhat cryptic species. This species, together with *P. ketele* (described above), forms an addition to the cluster of New Guinea species centered around *P. setistylus.* The limits of variation within members of this group are still not very well understood, and further field study of them is desirable.

Sect. MARKGRAVIDENDRON Huynh & Stone

Pandanus sulawesicus B. C. Stone, sp. nov. FIGURE 4.

Arbor, stipite in basi radicibus aereis rigidis emittens. Folia lineari-loriformia, apice abrupte acuminato breve-caudata, basi sensim angustata, profunde canaliculato; marginibus in basi spinulosis, spinulis curvato-patentibus curvatis acutis, ca. 4 mm longis, rariter duplicatis, 2–5 mm sese separatis, in medio cum spinulis 2.5 mm longis, 7–9 mm sese separatis, apicem versus spinulis ca. 1 mm longis, 0.6–3 mm (vel usque ad 12 mm) sese separatis; costa media in basi spinulis reflexis vel recurvatis ca. 4 mm longis, 2–5 mm sese separatis, in medio inermis, profunde et acute carinata, vel sparse et irregulariter pauci-spinulosa, spinulis antrorsis, apicem versus, spinulis antrorsis ca. 1 mm longis, confertioribus, ca. 4–5 mm sese separatis, in cauda densiter congestis, vix 1 mm sese separatis; nervis longitudinalibus ca. 0.75–0.9 mm sese separatis, infra leniter prominulis, ca. 86 per foliam (costa media excluso), apicem versus cum venulis transversis ca. 2–3 mm remotis connectis. Inflorescentia foeminea pedunculata; cephalium solitarium, oblongo-cylindraceum, ca. 19 × 9 cm, plurimis drupis compositum. Drupa irregulariter cuneata, apice truncato, (33–)36–40 mm longa, pileo indistincto integri, quinque- vel sexangulato, ca. 15 mm lato, vertice plano vel subdepresso, stylo perbreve ad latum areolis verticis posito, sursum spectantio; stigma ca. 3 × 3 mm, oblique vel verticaliter situato, aperturo centrali, margine minute denticulato, denticulis superioribus 3 vel 5, inferioribus 5 vel 8. Mesocarpium apicale ca. 8 mm longum cavernosum; basale

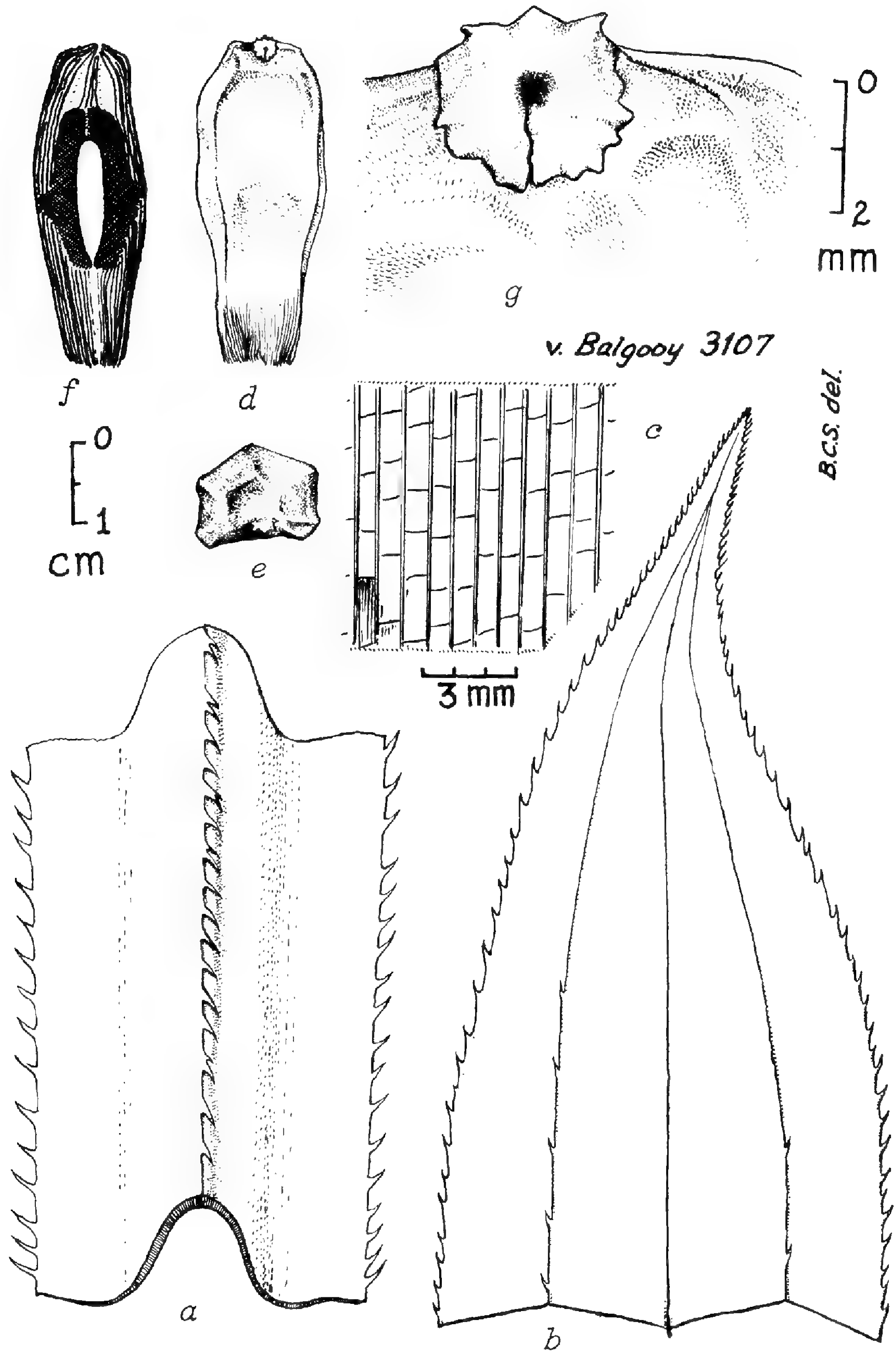


FIGURE 4. **Pandanus sulawesicus** (from *Van Balgooy 3107,* type collection). a–c, leaf: a, base, abaxial surface; b, apex, adaxial surface; c, detail of venation, showing transverse commissures. d–f, drupe: d, side view; e, top view; f, longitudinal section. g, stigma, enlarged, frontal view.

fibrosum ca. 12–15 mm longum. Endocarpium centrale ca. 20 mm longum uniloculatum apice rotundato basi truncato, pariete ca. 3 mm crasso parte medio toruloso 4–5 mm crasso excepto. Cetera ignota.

TYPE. Indonesia, Sulawesi, ca. lat. 1°S, long. 120°E, Sopu Valley, 85 km SSE of Palu, 1000 m alt., rainforest on flat, very wet alluvial soil; stilt-rooted pandan, fruit orange; May 1979, *Van Balgooy 3107* (holotype, L!).

This is the second member of sect. MARKGRAVIDENDRON, formerly a monotypic section consisting only of *Pandanus navicularis* Stone (endemic to New Ireland in the Bismarck Archipelago).

In its leaves, *Pandanus sulawesicus* is reminiscent of *P. cheilostigma* Stone and *P. brevistipes* Martelli, both of sect. CHEILOSTIGMA Stone, but the fruit characters are quite different. Sect. CHEILOSTIGMA is endemic to the Philippines.

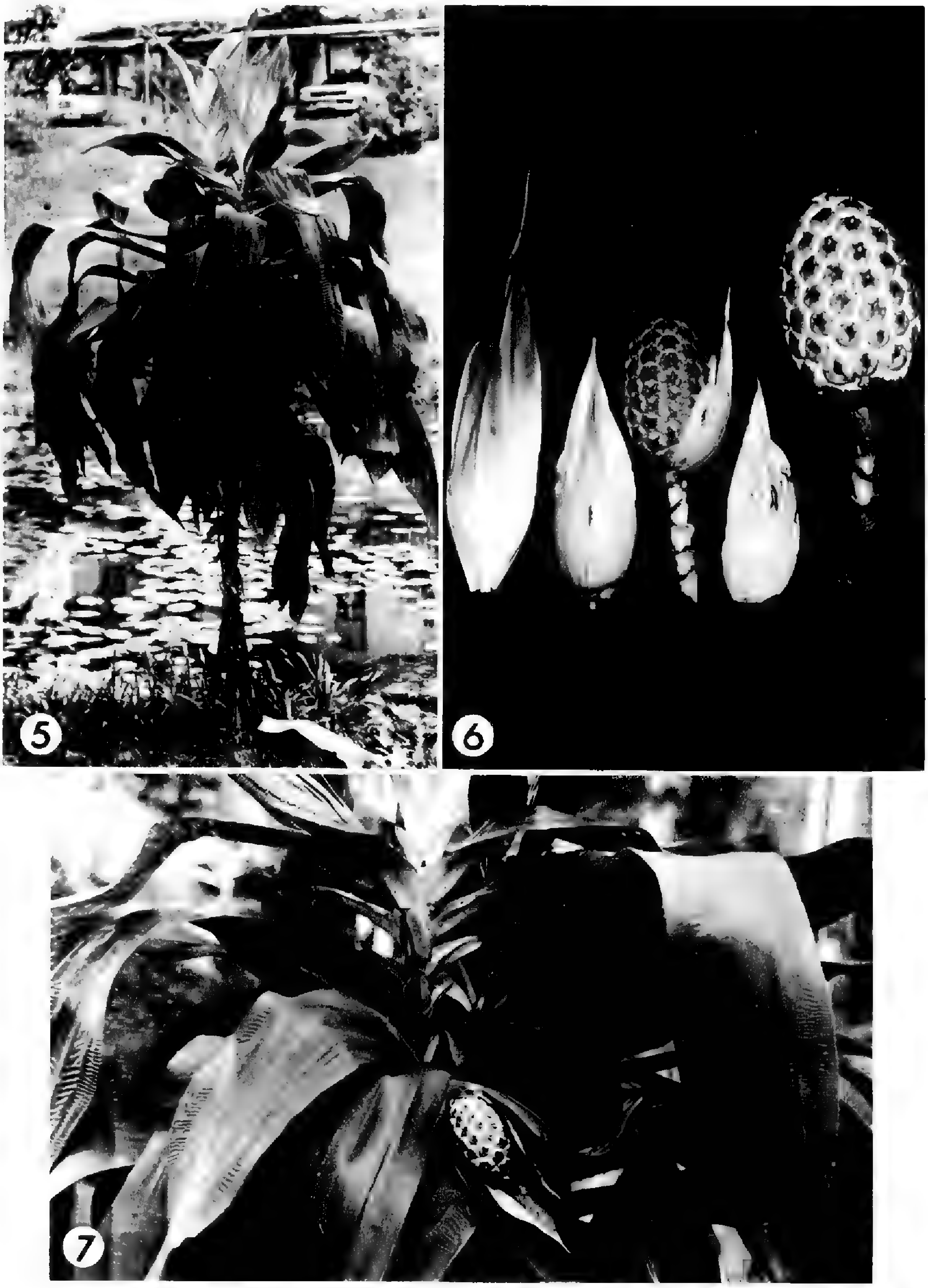
Sect. RYKIA (DeVriese) Kurz

Pandanus albifrons B. C. Stone, sp. nov. FIGURES 5–7.

Frutex simplex vel sparse ramosus usque ad 2–3.5 m altus, stipite angusti radicibus aereis paucibus brevibusque emittenti. Folia perlata, arcuata, usque ad 90–100 × 12–14 cm, acuminato-brevicaudata, basi conspicue angustata infra albo-glaucescentia; vaginis auriculatis, auriculis usque ad 10–11 × 1 cm; marginibus in basi unguiculatis dentibus antrorsis patentibus curvatis ad 3–4 mm longis, 5–20 mm sese separatis, in parte medio dentibus remotissimis 1–2 mm longis, (20–)30–50(–60) mm sese separatis, depressiter antrorsis, in apice denticulis vix 1 mm longis, 1–5 mm sese separatis; costa infra in parte brevi basilari retrorse hamato-spinosa spinis 3–4 mm longis, 5–15 mm sese separatis, costa deinde pro maxima parte mediani apicem versus et caudem excepta exarmata obscure carinata, in apice denticulatis, denticulis antrorsis vix 1 mm longis, 2–4 mm sese separatis; pagina laminae utrinque apicem versus minute tessellata, nervis longitudinalibus ca. 100 ad 105 per foliam, venulis transversis ca. 0.6–0.7 mm sese separatis. Inflorescentia terminalis, pedunculo foemineo ca. 15 cm longo, 7 cm diametro, bracteatis, bracteis albidis exterioribus usque ad 23 × 6–7 cm, interioribus ovato-navicularibus breviter caudatis ca. 8 × 4 cm. Cephalium solitarium ellipsoideum e 90 ad 100 drupis compositum, ca. 12 × 7.7 cm, flavidum. Drupa obovoideo-cuneiforma ca. 25 × 14 × 11–12 mm, pileo depresse-pyramidato hexagonato, stylo brunneo, 4–5 mm longo, centrali, antrorse deflecto, 1- vel 2-cornulato, cornulis ca. 1–2 mm longis stigmate nigro. Pericarpium subcarnosum flavidum. Mesocarpium superum medulloso-fibrosum ca. 8–10 mm longum; inferum fibroso-carnosum ca. 5–7 mm longum. Endocarpium inverso-cupuliforme apice in prolongatione centrali erecti, basi leniter angustato, infra centro positum, ca. 8 mm longum (corno centrali excepta), atro-brunneum, pariete ca. 1 mm crasso. Cetera ignota.

TYPE. Malaysia, Kepong Forest Research Institute, plants introduced from Pasoh Forest Reserve (Negri Sembilan); fruiting; November 1978, *Stone & Ng 14003* (holotype, KLU!; isotypes, BISH, K, KEP, L, SING, US).

This handsome species belongs to the group including *Pandanus crinifolius*



FIGURES 5–7. **Pandanus albifrons:** 5, type tree; 6, bracts and 2 cephalia from type tree; 7, type tree with exposed cephalium (note new shoot with white leaf bases in upper center).

Martelli (Malaya), *P. leuconotus* Stone (Borneo), and *P. nervosus* Stone (Sumatra). It is most similar to *P. leuconotus*; both have remarkable white leaf undersurfaces that are particularly conspicuous at the base of the leaf. The new species differs from *P. crinifolius* in its whitish leaf-base undersurfaces, white or off-white floral bracts, less crispate blades, and longer styles; from *P. leuconotus* in its more abruptly rounded-acuminate leaf tips, white or off-white spathes, and broader laminae; from *P. nervosus* in its wider leaves, more ellipsoid cephalia, and whiter spathes; and from all these species in its very remote marginal prickles along the median part of the leaf.

Although clearly related to such other species as *Pandanus unguifer* Hooker f., *P. tonkinensis* Stone, *P. dictyotus* St. John ex Stone, and *P. huynhii* Stone, *P. albifrons* is distinguished by several characters, especially the very broad, loriform leaves with the undersurfaces white near the base and broad auricular basal margins, and the white (vs. pink or yellow) floral bracts. The staminate plants of *P. albifrons* are still unknown, but they should strongly resemble those of *P. leuconotus,* undoubtedly the most closely related species.

Pandanus dictyotus St. John ex Stone, sp. nov.

Frutex humilis, habitu Pandanus crinifolio vel parviore. Folia lineari-loriformia, apice acuminata subabrupte caudata, basi leniter angustata; vaginis purpurascentibus; laminis ca. 80 × 6 cm, striatulo-nervosis, apicem versus evidenter tessellatis, cauda subulato-filiforma ca. 5 cm longa terminatis; marginibus in basi cum denticulis patentibus leniter arcuatis 2–3 mm longis, vulgo 10–25 mm sese separatis, in medio subinermis, apicem versus denticulis antrorse curvatis ca. 1 mm longis, 1–3 mm sese separatis; costa media dorso in basi paucidenticulatis, denticulis retrorsis, 2–3 mm longis, deinde erectis, subinermis, in medio inermis, apicem versus denticulis eis in margine adjacentio similibus. Inflorescentia terminalis, brevis, pedunculo foemineo ca. 7.5 cm longo, 5 mm crasso, apice incrassato, bracteato, bracteis superioribus congestibus ovato-ellipticis brevicaudatis, marginibus minute serrulatis; cephalio subellipsoideo ca. 7 × 4.5 cm, drupis simplicibus composito; drupa ca. 18–20 mm longa, pileo hemispherico pyramidato, stylo centrali antrorse curvato, subulato, ca. 4 mm longo, 1- vel 2-cornato, cornulis brevibus vix 1 mm longis.

TYPE. Sarawak, Bako National Park, March 1961, *S 13017, Rashid b. Taggoi* (holotype, SAR!).

A small shrub of lowland forest. For taxonomic comments, see under *Pandanus albifrons.*

Pandanus leuconotus B. C. Stone, sp. nov. FIGURE 8.

Frutex; stipite erecto usque ad 2.5 m alto e basi radicibus brevibus paucibus emittenti. Folia late loriformia arcuata, basi modice attenuata ad apicem acuminato-caudata usque ad 120 × 9.5 cm, tessellato-reticulata (in sicco), infra in parte basilari conspicue glauco-alba, marginibus toto denticulatis, denticulis maximis ad 7 mm longis, antrorsis; costa infra in basi denticulis reflexis armata.

Inflorescentia terminalis, cephalio druparum breve oblongo 10–12.5 × 6–7 cm, obscure trigonato, drupis 25–30 × 9–11 mm, pileo truncato-pyramidato, stylo castaneo uni- vel rariter bicornato 4–5 mm longo antrorse valde deflecto, endocarpio 10 mm longo, pariete 1 mm crasso. Spadix masculus bracteata, spathis fertilibus 7 usque ad 35 cm longis, spicibus oblongis albis 5–7 × 1.5 cm, phalangibus staminorum umbellatis columnis 3–5 mm longis, filamentis ca. 1 mm longis, antheris 1–1.2 mm longis apiculatis, apiculo 0.9–1.1 mm longo.

TYPE. Borneo, Sabah, Ranau District, Poring, base of Mt. Kinabalu, 330 m alt., in forest near Hot Springs, April 1975, *B. C. Stone et al. 12906* (holotype, KLU; isotypes, BISH, K, L, SAN).

ADDITIONAL SPECIMENS EXAMINED. **Borneo.** SABAH: Mt. Kinabalu, Dallas, ca. 900 m alt., *J. & M. S. Clemens 27751* (UC!), *J. & M. S. Clemens 26857* (A!, BO!); Mt. Kinabalu, 330 m alt., *Stone 12905* (KLU).

This species is similar in overall appearance and many particulars to *Pandanus albifrons* (described above), of the Malay Peninsula, and shares the white coloration of the leaf-base undersurface with that species, which is manifestly its nearest relative. It is also related to *P. crinifolius* and, a little more distantly, to *P. tonkinensis* Stone. For further details, see the comments after *P. albifrons.*

Plants of *Pandanus leuconotus* have been brought by Kinabalu National Park workers from nearby places and planted in the Poring Hot Springs area, where they thrive, flowering and fruiting regularly.

Pandanus nanofrutex B. C. Stone, sp. nov.

Frutex nanus. Corona foliorum compacta. Folia linearia angusta usque ad 95 × 2.8 cm, apice acuminato vel breve-caudato, basi leniter angustata; marginibus denticulatis, in basi denticulis 2–3 mm longis, 5–12 mm sese separatis, in medio denticulis ca. 1 mm longis, appressis, antrorsis, ca. 5–14 mm sese separatis, apicem versus denticulis 0.5–0.75 mm longis, vulgo 1–2 mm sese separatis; costa media basem versus denticulis retrorsis 2–3 mm longis, vulgo 10–20(–35) mm sese separatis, in medio (parte tertio folii) inermis, carinatis, apicem versus denticulis antrorsis 1 mm longis, 5 mm sese separatis, et in cauda vix 2 mm sese separatis; venis longitudinalibus angustis, prominulentibus, 0.5–0.6 mm sese separatis, ca. 50 per foliam; venulis transversalibus prominulentibus, reticulationes subisolateralibus formantibus, areolis vix 1 mm longis. Inflorescentia terminalis, erecta, cephalio solitario oblato-globoso ca. 60 × 50–55 mm, pedunculo ad 14 cm longo angusto, apicem versus incrassato 7 mm crasso; bracteis usque ad 12 × 4 cm, abrupte acuminato-subcaudatis, apicem versus in margine costaque minute spinulosis; receptaculo ca. 20 × 20 mm. Drupae ca. 85 ad 95 per cephalio, 18–22 mm longae stylo excluso (ad 27 mm longo stylo incluso), 10–12 mm latae; pileo subhemisphericо-pyramidale, 3–5 mm alto; stylo centrali, erecto vel antrorse deflecto, haud vel minime furcato, subtereti vel compresso, 5–6 mm longo, deltoideo-acuto, furcis ca. 1 mm longis; stigmate ca. 4 mm longo, ovato-elliptico. Mesocarpium superum medullosum, inferum fibrosum subcarnosum. Endocarpium central-

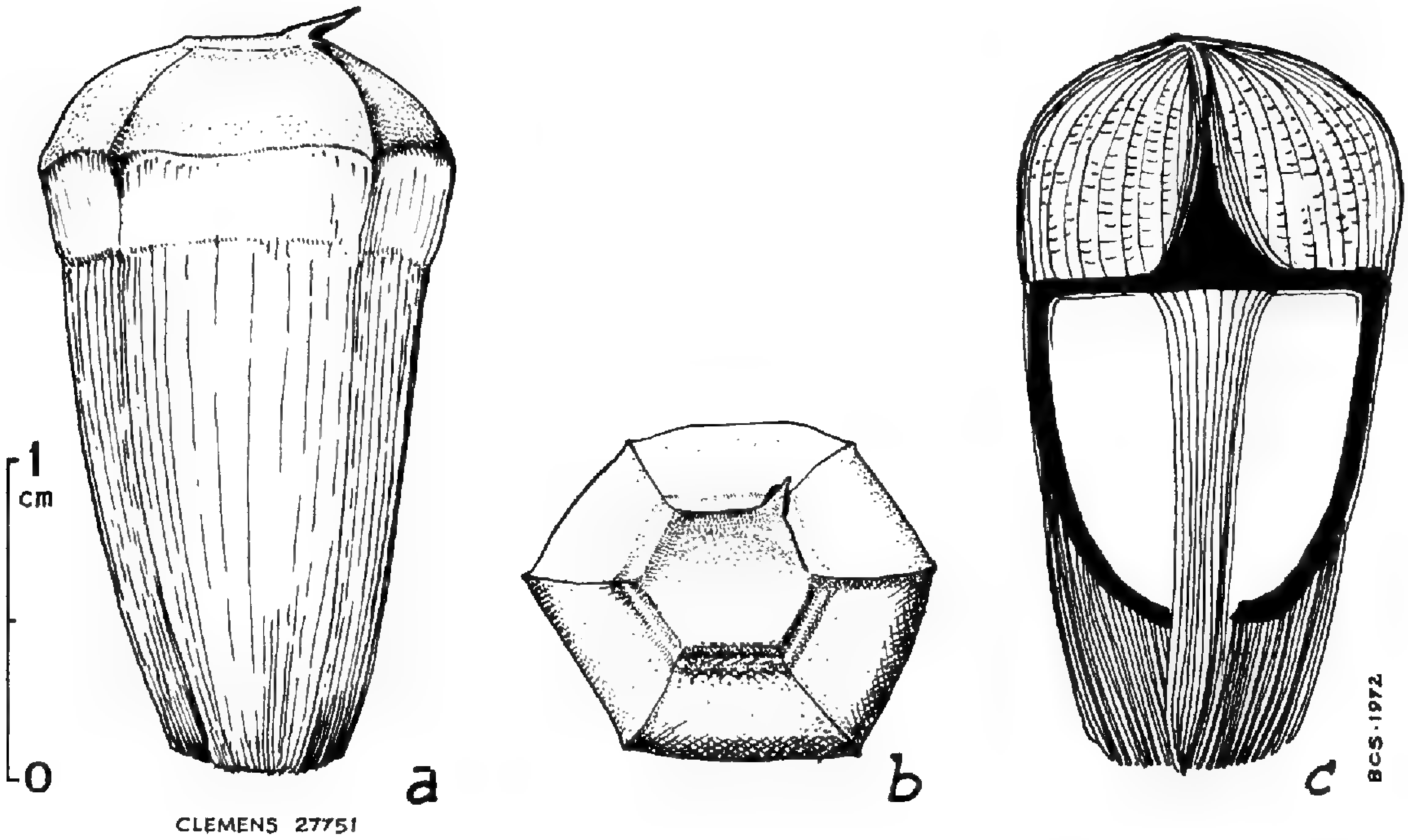


FIGURE 8. **Pandanus leuconotus** (from *Clemens 27751*), drupe: a, side view; b, top view; c, longitudinal section.

ium ca. 8 mm longum, apice conico-elongato, atrobrunneum, osseum, pariete ca. 1 mm crasso, loculo singulo.

TYPE. Tonkin [Vietnam, Hà Son Binh Province], Mt. Ba Vi, vallée du Lankok, dans les fôrets, Janvier 1889, *Balansa 4165-bis* (holotype, P!).

This species stands out among the members of sect. RYKIA because of its dwarf, shrubby stature, its narrow leaves with large marginal prickles, and its small fruit-heads. Martelli had determined the type specimen previously as *Pandanus stenophyllus* Kurz (= *P. nitidus* (Miq.) Kurz), a Javanese species of sect. ASTERODONTIA Stone and not very closely related. Instead, *P. nanofrutex* belongs to a small group of species within sect. RYKIA that includes *P. unguifer, P. bicornis* Ridley, *P. huyhnii,* and some others that occur in southeastern Asia and western Malesia. It is quite similar to *P. bifidus* St. John, of Thailand, but differs in its smaller cephalia and drupes, its shorter style-forks, and its considerably shorter leaves.

Pandanus nervosus B. C. Stone, sp. nov.

Frutex. Folia usque ad 100 × 11 cm, versus apicem perabrupte rotundata, apice acuminato-caudata, caudis ca. 9 cm longis; marginibus valde armatis, dentibus usque ad 3–4 mm longis, in caudo dense congestibus multo minoribus ca. 1 mm longis; pagina utrinque valde reticulato-tessellata; costa basi dentibus retrorsis usque ad 5 mm longis, 1–2 cm sese separatis, dispositis. Inflorescentia terminalis, foemineo solitario, cephalio subgloboso, ca. 7 × 5 cm, e ca. 80 ad 90 drupis composito, pedunculato; drupis uniloculatis, 15–18 × 6–9 mm vel usque ad 22 × 13 mm, 5- vel 6-angulatis, apice subtruncato-subdepresse pyramidato, stylo 1- vel 2-cornuto, ca. 3–5 × 4–6 mm, cornis acicularibus 1–2 mm longis divergentibus vel valde divaricatis; endocarpio cupulato apice in acumine anguste conico breviter prolongato ca. 15–16 mm longo terminato. Cetera ignota.

TYPE. Sumatra, east coast, vale of Tangga, Asahan, May 1927, *H. H. Bartlett 8057* (holotype, US!).

ADDITIONAL SPECIMENS EXAMINED. **Indonesia.** SUMATRA: Asahan, Goerach Batoe, swampy places in forest, *Yates 1653* (UC!); west coast, Bukit Baloe Banting, 1100 m alt., *Jacobson 195* (BO!); Asahan, vic. of Taloen Djoring, Silo Maradja, Dec. 1927, *Rahmat si Toroes 39* (A!, MICH).

This is a very characteristic species known so far only from Sumatra.

The Jacobson collection included living plants (or seeds) that were subsequently grown in the Botanical Gardens, Bogor (now known as Kebun Raya, Indonesia). Specimens were later collected (in September 1932) from the cultivated plants. There is a whole fruit-head preserved in alcohol in the carpological collection there.

Pandanus regalis B. C. Stone, sp. nov. FIGURES 9, 10.

A Pandanus furcato affini sed cephalio perelongato trigono-subcylindrico usque ad 100 × 25 cm, plurimis drupis composito; drupis ca. 38–40 × 10 mm, pileis pyramidato-rotundatis; stylo aceroso vel furcato; mesocarpio supra fibroso-medulloso, infra fibroso-subcarnoso; endocarpio osseo atrobrunneo-ferrugineo apice acute pyramidato base truncato fere totam corpam drupae occupanti, ca. 27 mm longo, pariete ca. 2 mm crasso. Semen unicum.

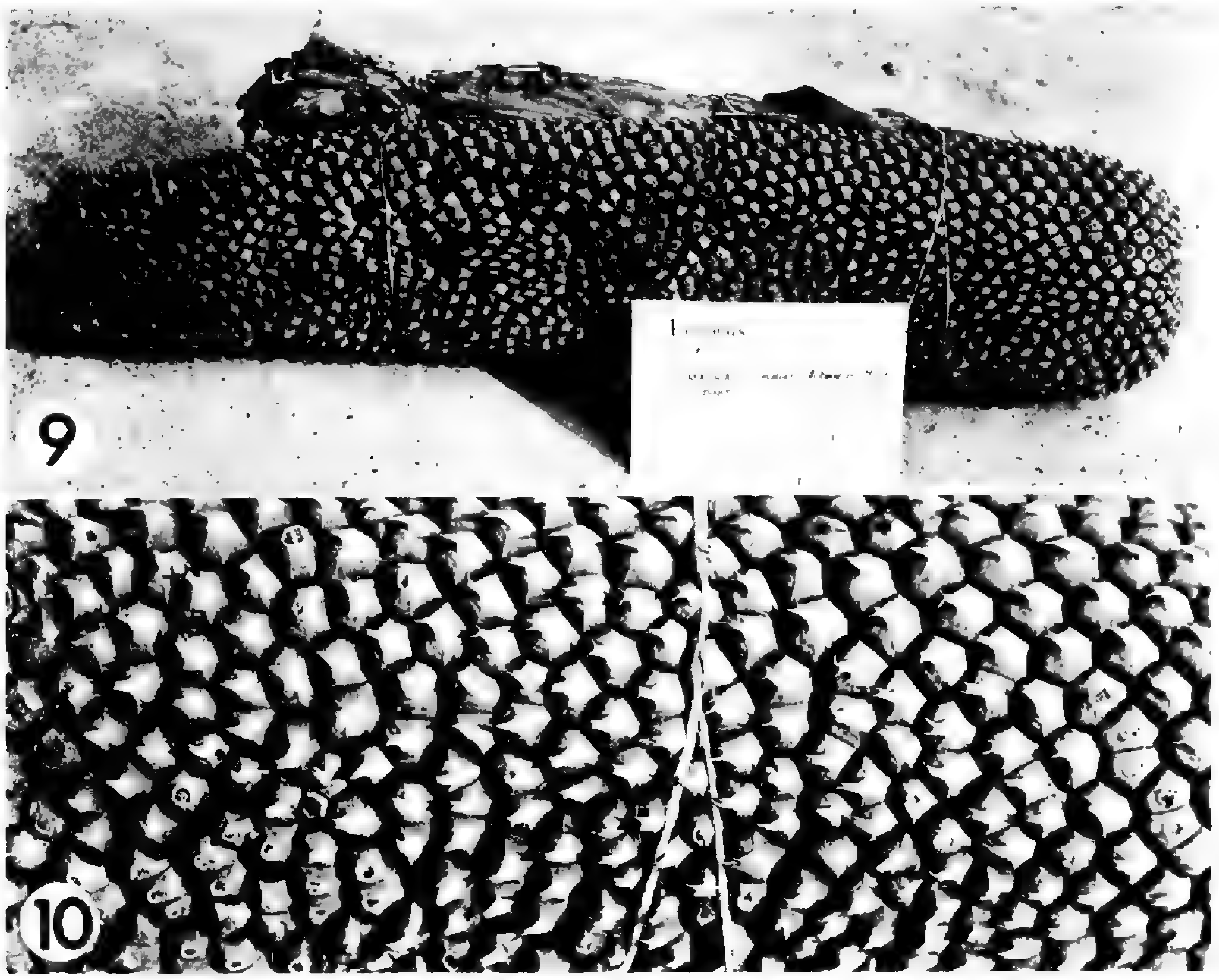
TYPE. Sumatra, Simaloer Island, Feb. 1919, *Achmad 909* (BO!).

No other material has been seen of what is certainly an imposing species. Although the leaf specimens in particular are only fragmentary, they give the impression of being from a very large plant. The middle portion of an adult leaf is 10.5 cm wide, with marginal prickles ca. 4 mm long and about 5–6 mm apart; another part of the leaf closer to the apex is nearly 8 cm wide, narrowing distally to 6.5 cm, with similar but closer clydoniform prickles. The fruit-head is longer than that of almost any other *Pandanus* species known to me, and the drupes are stocky and almost parallel sided.

Certainly this is a very distinctive plant. Nevertheless, it is clearly among the species closely related to *Pandanus furcatus* Roxb.

Pandanus tonkinensis B. C. Stone, sp. nov.

Frutex humilis, stipite usque ad 15 mm diametro; corona foliorum compacta. Folia ca. 50–90 × 4 cm, apice acuminato-caudata, basi leniter angustata, parte vaginanti maturitate cupreo-brunnea; marginibus in basi cum denticulis patentibus ca. 4 mm longis, 10–22 mm sese separatis, in medio cum denticulis 2–3 mm longis, usque ad 33 mm sese separatis, apicem versus denticulis ca. 1 mm longis, 2–5 (vel in caudo 1) mm sese separatis; costa media in basi denticulis retrorsis 4–5 mm longis, 10–15 (deinde ad 30) mm sese separatis,



Figures 9, 10. **Pandanus regalis** (from *Achmad 909,* type collection): 9, entire infructescence; 10, detail of same, showing drupe apices and forked styles.

in parte tertio medio inermi, apicem versus denticulis antrorsis ad eos in margine adjacentio similibus, in caudo extremo remotioribus; nervis longitudinalibus manifestis, cum venulis transversalibus reticulationibus tessellatis formantibus; lamina vulgo 48- ad 50-nervatis, nervis ca. 0.8–0.9 mm sese separatis. Inflorescentia terminalis, pedunculo ad 14 cm longis, apice 9 mm crasso, triquetro, bracteato; cephalium solitarium globosum maturitate ca. 55 × 50 mm, e ca. 70 drupis compositum; receptaculo ca. 15 × 10 mm; drupis obovoideis, ca. 25–27 × 10 mm, drupis basalibus exceptis (eis ca. 17 × 10–11 mm); pileus 3–5 mm altus, depresse pyramidatus, stylo centrale erecto vel antrorse deflecto rubro-brunneo nitido 4–5 mm longo subtereti vel compressi 1- vel 2-cornato instructo; furcibus stylorum vix 1 mm longis, acutis; mesocarpium superum medullosum, inferum fibroso-subcarnosum; endocarpium ca. 10 mm longum, apice in rostro subconico-centrale producto, 1-loculatum pariete ca. 1 mm crasso, osseo, atroferrugineo.

Type. [Vietnam], Dac Lac [Darlac] Province, SE of Poste du Lac, 1200 m alt., April 1921, *Poilane 32462* (holotype, p!).

Additional specimens examined. **Vietnam.** Hà Son Binh Province: Mt. Ba Vi, 1000 m alt., *Balansa 4165* (p!); Broyi, *Hayata 5211* (p!). Nha Trang [Phu Khanh] Province: Nui-han-heo, *Poilane 4888* (p!). Quang Tri [Binh Tri Thien] Province: Col d'Ailao et Dent du Tigre, 1500 m alt., *Poilane 10403* (p!).

This taxon was segregated first by Martelli and was described, but only in

French, in H. Lecomte (Fl. Gén. Indo-Chine **6**: 1063. 1937). No Latin diagnosis was ever published. Because *Pandanus nanofrutex* (described above) was among the specimens ascribed to *P. tonkinensis* by Martelli, it seems preferable to publish the latter as a new species here.

Pandanus tonkinensis is closely related to certain species of sect. RYKIA with small or even dwarf stature, small fruit-heads, leaves often noticeably contracted toward the base and usually abruptly acuminate-caudate at the apex, and drupes with usually forked styles. This group includes such species as *P. unguifer, P. bicornis, P. huyhnii,* and *P. nanofrutex.* These, and perhaps some others from Thailand, form a complex in which species distinctions are often obscure, perhaps mostly because of the very few and often inadequate collections made. For most, the staminate plants remain unknown. Basic to any improvement in our knowledge of this group, therefore, is a continued effort to obtain good collections supplemented by field observations and photographs.

DEPARTMENT OF BOTANY
UNIVERSITY OF MALAYA
KUALA LUMPUR, MALAYSIA

A NEW LINDERA (LAURACEAE) FROM NORTH AMERICA[1]

B. EUGENE WOFFORD

THE GENUS *Lindera* Thunb., composed of upwards of 100 species, is primarily of eastern Asia (Wood, 1958), with only three species in North America. *Lindera benzoin* (L.) Blume (including *L. benzoin* var. *pubescens* (Palmer & Steyerm.) Rehder), the most common and widespread North American taxon, ranges generally throughout eastern North America from Maine, southern Ontario, and southern Michigan southward, and westward into Kansas, Oklahoma, and Texas. It occurs in mesic habitats along shaded streambanks and in damp woods and bottomland swamps. *Lindera melissifolia* (Walter) Blume, a rare and local species, inhabits mesic to hydric sites (i.e., bottomland hardwoods, depressions, and margins of sandy sinks and ponds). Extant populations are presently known from the Coastal Plain of North Carolina, South Carolina, Georgia, Mississippi, and along the Arkansas-Missouri state line (MAP 1). Populations from Alabama (Wilcox Co., *Buckley s.n.*, GH!, NY!, US!), western Florida (without specific locality, *Chapman s.n.*, NY!), and Louisiana (without specific locality, *Hale s.n.*, GH!) have not been seen in over a century and are probably now extirpated from these states. The nomenclatural history, ecology, distribution, and morphological features for separating *L. melissifolia* from *L. benzoin* were elucidated by Steyermark (1949).

During herbarium studies in preparation for a forthcoming treatment of Lauraceae for the *Vascular Flora of the Southeastern United States* (J. R. Massey, ed.), I encountered great difficulty in placing a number of collections of *Lindera* within the circumscription of either *L. benzoin* or *L. melissifolia*. Most of these collections were made from the Mississippi Gulf Coastal Plain by Drs. Sidney McDaniel and Ken E. Rogers. Subsequent field and herbarium studies have led me to conclude that these specimens are representative of a new species, described here.

Lindera subcoriacea B. E. Wofford, sp. nov. FIGURE 1.

Frutex parvus, ad 2 m alta, dioecious. Folia subcoriacea, vix aromatica, elliptica vel oblanceolata, 4–7.5 cm longa, 2–3.5 cm lata, apice obtusa vel rotunda. Drupa vivida rubra, ca. 10 mm longa, elliptica.

Dioecious, deciduous shrub to 2 m. Stems smooth, light gray and pubescent when young, becoming darker gray and glabrous with age. Leaves with petiole canaliculate, 3–10 mm long, pubescent; blade subcoriaceous, horizontal to ascending, elliptic to oblanceolate, 4–7.5 by 2–3.5 cm (lower stem leaves re-

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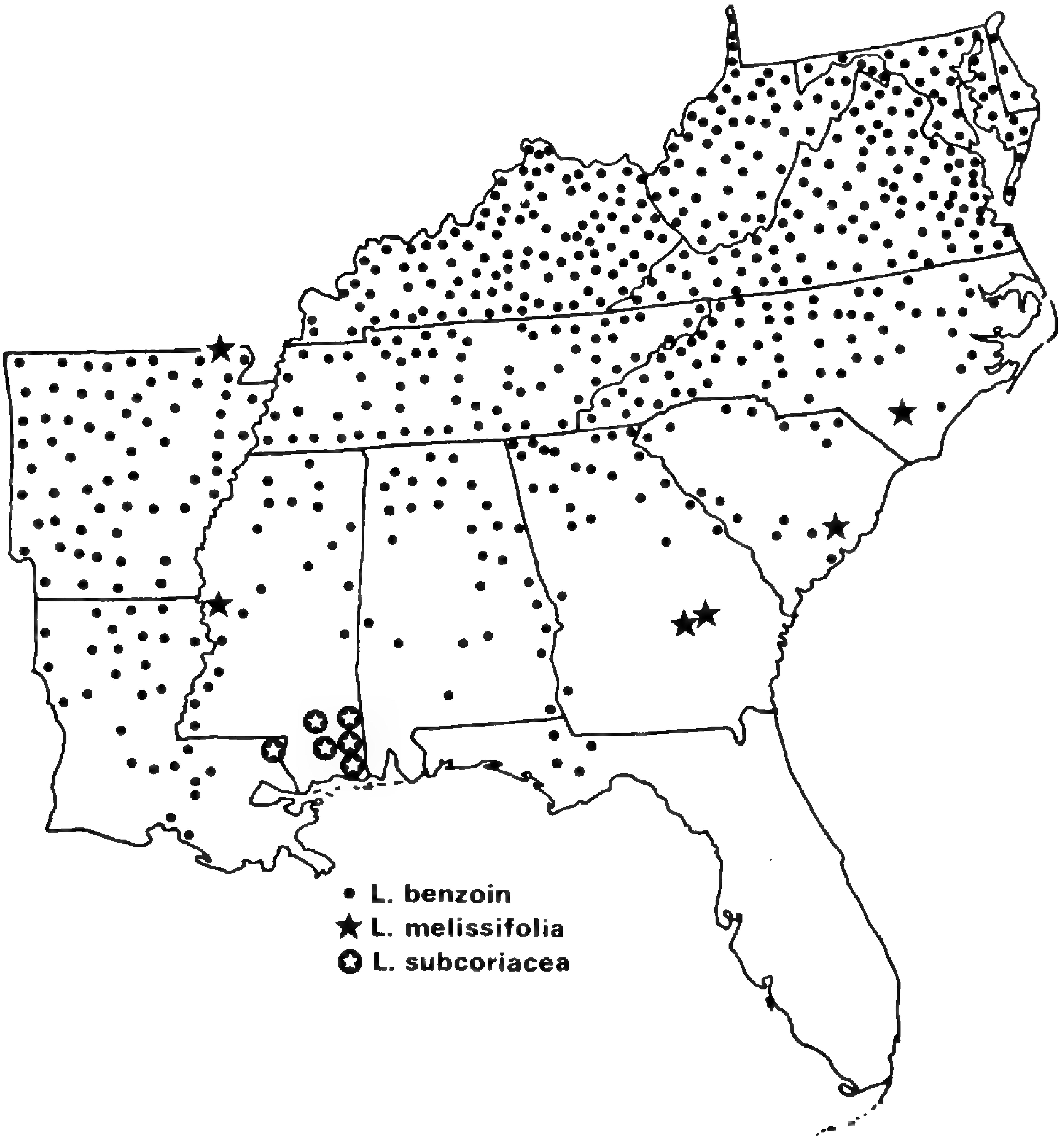
[1] Contributions from the Botanical Laboratory, The University of Tennessee, N.S. No. 543.

Journal of the Arnold Arboretum 64: 325–331. April, 1983.



MAP 1. Distribution of **Lindera** in the southeastern United States.

duced), the apex obtuse to rounded, rarely slightly acuminate (mucronulate when young), the base cuneate, the margin entire (ciliate when young), the venation eucamptodromous, the lower surface pale green, glaucescent, moderately pubescent, the upper surface darker green, pubescent when young, becoming essentially glabrous with age. Flowers appearing before leaves in axils of preceding year's leaves on stout, supraaxillary branches 1.5 mm long and terminated by vegetative bud; inflorescences of 1 to 4 umbellike cymose clusters, each cluster 3- or 4- (rarely 5-)flowered, subtended by 2 pairs of concave, decussate, coriaceous, deciduous bracts, with outer pair 2.5 by 3 mm, inner pair 3 by 3.5 mm, the secondary bracts caducous, tepaloid, reduced. Flower buds globose, ca. 2.5 mm wide; flowers imperfect, regular; tepals 6, 2.2 mm by 1.8 mm, glabrous, pellucid-punctate, perianth tube short. Staminate flowers on pedicels to 4 mm long; stamens 9, introrse, 2-locular, yellow, those of series

I and II similar, 2.5 mm long, with anther 1 by 1 mm, those of series III 2.5 mm long, filament broadened, each with pair of conspicuous glands at base, those of series IV lacking; pistillodium 1.2 mm long. Pistillate flowers on pedicels to 1.5 mm long; tepals slightly smaller than those of staminate flowers; stamens variously developed, often reduced to glands resembling those at base of series III stamens of staminate flowers; stigma papillose, style 1 mm long, the ovary elliptic, 1 by 0.6 mm. Drupes bright red, ca. 10 mm long, elliptic, borne on pedicels to 4 mm long.

Type. Mississippi, George Co., hillside bog 1 mi NW of Escatawpa River and 100 yd SW of Hwy. 98, 27 July 1982, *B. E. Wofford 82-121, with D. L. Scott & M. G. Lelong* (holotype, A; isotypes, IBE, NY, RSA, TENN, VDB).

Distribution and phenology. Open areas of permanently wet, peaty, evergreen shrub bogs on Gulf Coastal Plain of Mississippi and Louisiana (Map 1). Flowering in mid-March; fruits maturing in late fall.

Specimens examined. **Louisiana.** Washington Parish: swampy woods beside La. 10 and Lawrence Creek, 2 mi E of Franklinton, sect. 29, T. 2 S, R. 11 E, *Thomas et al. 32367* (NLU). **Mississippi.** Forrest Co.: ca. 100 yd W of Hwy. 49, S of Hattiesburg ca. 7 mi from jct. of hwys. 98 and 49, S border of artificial pond, *Rogers 4932* (MISS). George Co.: 5.5 mi S of Agricola, common shrub in quaking bog, *McDaniel 4165* (FSU, IBE); 5.5 mi S of Agricola, *McDaniel 10345* (FSU, IBE, Miss. Mus. Nat. Sci., SMU), *10348* (FSU, IBE); quaking bog 5.5 mi S of Agricola, W side of Hwy. 613, sect. 32, T. 3 S, R. 5 W, *Gordon 2576* (Miss. Mus. Nat. Sci.); peat bog 5.5 mi S of Agricola and ca. 0.3 mi N of George/Jackson Co. line on W side of Hwy. 613, *Wofford 82-3* (TENN); boggy area on open hillside along S side of Hwy. 98, ca. 0.5 mi W of Alabama-Mississippi state line, NW¼ sect. 20, T. 2 S, R. 4 W, *Lelong 5199* (NCU); at Mississippi-Alabama line off Hwy. 98 ca. 200–300 yd S of hwy., *Rogers 2902* (MISS, MO, NCU); bog in longleaf pine woods S of U. S. 98 just W of Alabama state line, *Thomas et al. 43060* (LSU, NLU); Shipman bog, Wilmer Quad., sects. 18 (SW¼), 19 (NW¼), 13 (SE¼), T. 1 S, R. 4 W, *Rogers 45917* (TENN); 0.8 mi NW of Escatawpa R. off Hwy. 98 to Lucedale, *Lelong s.n.*, 3 April 1981 (TENN); ca. 0.8 mi W of Mississippi-Alabama state line on Hwy. 98, SE¼ sect. 13, T. 2 S, R. 5 W; SW¼ sect. 18, T. 2 S, R. 4 W, *Gordon et al. 2552* (Miss. Mus. Nat. Sci.); hillside bog ca. 0.8 mi W of Mississippi-Alabama line S of Hwy. 98, *Gordon & Burris 2749* (Miss. Mus. Nat. Sci.); Wilmer Quad., 1 mi NW of Escatawpa R. then 100 yd SW of Hwy. 98, *Wofford et al. 81-47* (A, TENN); upland bog ca. 1 mi W of Escatawpa R. and 100 yd SW of Hwy. 98, *Wofford et al. 82-1* (TENN). Greene Co.: acid bog 2 mi SE of Leakesville, Hwy. 63, *Jones 8484* (FSU, MISS); bluff SE of Chickasawhay R. at Leakesville, *Jones 11225* (FSU, MISS). Jackson Co.: evergreen shrub bog, ca. 1.5 mi W of LaRue and ca. 100 yd W of dirt road, sect. 23, T. 5 S, R. 9 W, *Wofford 82-2* (TENN). Stone Co.: Toc-O-Leen Lake, sect. 20, T. 2 S, R. 13 W, *Rogers 8769* (MO, NCU, NY, SMU, USF).

Salient features for recognizing *Lindera subcoriacea* include its subcoriaceous, elliptic to oblanceolate leaves (obtuse to rounded at the tip) that are less than 7.5 cm long and only faintly aromatic. Although several primarily northern deciduous woody taxa tend to produce more coriaceous or semievergreen leaves near the southern limit of their ranges, the thickened leaves of *L. subcoriacea* appear to be a genetic divergence; *L. benzoin* leaves remain membranaceous at roughly the same latitude in Florida, southwestern Mississippi, and Louisiana. Other characters that can be used to separate the three North American taxa are summarized in Table 1.

FIGURE 1. Holotype of **Lindera subcoriacea** Wofford.

TABLE 1. **Character comparisons of the North American taxa of Lindera.**

CHARACTER	TAXON		
	L. subcoriacea	**L. benzoin**	**L. melissifolia**
Leaf			
Texture	Subcoriaceous	Membranaceous	Membranaceous
Length × width (cm)	4–7.5 × 2–3.5	6–15 × 3–6	8–16 × 3–6
Shape	Elliptic to oblanceolate	Obovate	Ovate to elliptic
Apex	Obtuse to rounded	Acuminate	Acute
Base	Cuneate	Cuneate	Widely cuneate to rounded
Pubescence (abaxial side)	Present	Present or absent	Present
Orientation	Horizontal to ascending	Horizontal to ascending	Drooping
Fragrance	Faint, piny lemon	Strong, "spicy"	Strong, sassafras-like
Fruit			
Length (mm)	10	10	12
Pedicel	Not thickened at apex; deciduous	Not thickened at apex; deciduous	Thickened at apex; persistent

Lindera subcoriacea is restricted to open areas of permanently wet, peaty, evergreen shrub bogs on the Gulf Coastal Plain of Mississippi and Louisiana. These highly organic, acidic microhabitats are fire dependent and offer abundant sunlight, moisture, and few competitors. In small (up to ca. 5 m in diameter) areas of deep peat accumulation, they simulate the "quaking" nature usually associated with the more familiar peat bog formations of cooler regions of the Northern Hemisphere. Dominant woody plant associates include *Cliftonia monophylla* (Lam.) Britton ex Sarg., *Magnolia virginiana* L., *Persea palustris* (Raf.) Sarg., *Myrica heterophylla* Raf., *M. cerifera* L., *Ilex glabra* (L.) A. Gray, *Hypericum brachyphyllum* (Spach) Steudel, and *Smilax laurifolia* L. Herbaceous associates are more variable in frequency and reflect the seral stage of each individual bog. Some of the more common of these include *Sarracenia alata* (Wood) Wood, *Oxypolis filiformis* (Walter) Britton, *Lophiola americana* (Pursh) Wood, *Sabatia macrophylla* Hooker, *Dichromena latifolia* Baldwin, *Zigadenus glaberrimus* Michaux, *Rhexia alifanus* Walter, *R. petiolata* Walter, *Polygala cruciata* L., *P. cymosa* Walter, *Fuirena squarrosa* Michaux, *Cacalia lanceolata* Nutt., *Muhlenbergia expansa* (DC.) Trin., *Panicum spretum* Schultes, *P. scabriusculum* Ell., *P. nudicaule* Vasey, *Stokesia laevis* (Hill) Greene, and *Eupatorium recurvans* Small.

Conversely, both *Lindera benzoin* and *L. melissifolia* occur on mostly shaded, mesic or slightly hydric sites but never in areas that are saturated throughout the growing season. In the southeastern United States *L. benzoin* is associated with taxa characteristic of shaded alluvial woods and eastern deciduous forests (e.g., *Acer saccharum* Marsh., *Liriodendron tulipifera* L., *Fagus grandifolia* Ehrh., *Aesculus glabra* Willd., *A. octandra* Marsh., *Sanguinaria canadensis* L., *Erythronium americanum* Ker-Gawl., *Claytonia virginica* L., *Polystichum acrostichoides* (Michaux) Schott, *Dentaria* spp., and *Trillium* spp.). Similarly, *L. melissifolia* occurs on mesic or slightly hydric sites that are occasionally inundated for several months during the growing season. Along the Mississippi Embayment in Mississippi and Arkansas, I have observed this taxon in low depressions of bottomland forests dominated by species of *Ulmus, Liquidambar, Celtis, Fraxinus,* and *Quercus.* Such forests are somewhat transitional in species composition between swamp forests and eastern deciduous forests. These local depressions, however, are often filled with dense clonal stands made up almost exclusively of *L. melissifolia* with essentially no characteristic herbaceous associates. On the Atlantic Coastal Plain *L. melissifolia* occurs around the margins of limestone sinks and pineland depressions. Competition with herbaceous associates, with the exception of *Woodwardia virginica* (L.) Sm. and occasional *Xyris* and *Eupatorium* spp. (R. Porcher, pers. comm.), is also minimal here.

Distributional and phenological data provide additional evidence for the recognition of *Lindera subcoriacea* as a distinct species. On the Gulf Coastal Plain it is disjunct from the nearest known population of *L. benzoin* by ca. 75 miles, and from the nearest population of *L. melissifolia* by ca. 150 miles (see MAP 1). Field studies in the spring of 1982 showed that *L. subcoriacea* reached peak anthesis on March 18–20, while the Mississippi population of *L. melissifolia* 150 miles to the north had flowered about seven to ten days earlier. More importantly, by March 21 nearby populations of *L. benzoin* in West Feliciana Parish, Louisiana, and Wilkinson Co., Mississippi (both at roughly the same latitude as *L. subcoriacea*), had half-expanded leaves, young fruits, and only a few scattered remnants of withered staminate inflorescences. Although more detailed phenological studies are needed, it is safe to conclude that existing geographic and phenological barriers preclude opportunities for gene exchange between *L. subcoriacea* and either *L. benzoin* or *L. melissifolia.*

Fragrances from crushed leaves and stems provide additional characters for species delimitation. *Lindera benzoin* emits a distinct and familiar "spicy" fragrance. *Lindera melissifolia* exudes an odor similar to that of sassafras (Steyermark, 1949; Godfrey & Wooten, 1981). Both of these fragrances are easily detected in fresh material throughout the growing season. *Lindera subcoriacea,* on the other hand, emits a scarcely detectable piny lemon fragrance when stems and leaves are young but becomes essentially odorless during late summer and fall. Analyses of these compounds are currently underway. Additional preliminary data from flavonoid studies show distinct interspecific chromatographic profiles from leaf extracts, with similar profiles from flower extracts. These data will be presented later.

In summary, *Lindera subcoriacea* can be separated from both *L. benzoin* and *L. melissifolia* on the basis of morphological, ecological, distributional, and phenological data. In morphological features (TABLE 1) it appears to be more closely related to (and perhaps shares a common ancestor with) *L. benzoin.* In ecological characters, however, its affinities differ: it shares a preference for more hydric sites with *L. melissifolia,* yet it requires open, sunny sites unlike those of either *L. benzoin* or *L. melissifolia.* It appears equally distinct from both taxa in distribution, phenology, and chemistry. Therefore, additional field studies along with chemosystematic and cytological data are needed before more definitive phylogenetic relationships can be theorized. Its closest relationships may prove to be among the numerous species of eastern Asia.

Finally, *Lindera subcoriacea* appears to be quite rare and in need of protection and habitat management. Additional plants have not been located at sites of several of the earlier collections, and some of the known populations are presently threatened by construction projects or occur on unprotected private land. Bog habitats, in general, are rapidly disappearing subsequent to man's control of naturally occurring seasonal fires combined with the construction of drainage ditches, farm ponds, and highways. Folkerts (1982) recently estimated that approximately 97 percent of the former Gulf Coast bog communities have been destroyed or seriously altered since pre-Columbian times.

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LÉON CAMILLE MARIUS CROIZAT(-CHALEY)

Turin, Italy—July 16, 1894
Coro, Venezuela—November 30, 1982

We record with regret the death of Dr. Léon Croizat, member of the staff of the Arnold Arboretum from 1938 to 1947 and student of the Euphorbiaceae.

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A REVISION OF THE GENUS ALSOPHILA (CYATHEACEAE) IN THE AMERICAS

DAVID S. CONANT

THE GENUS *Alsophila* R. Br. is here redefined based on the recent biosystematic studies of Conant (1975, 1976) and Conant and Cooper-Driver (1980). A major contribution to the understanding of the classification of the Cyatheaceae has been Tryon's (1970) separation of the scaly tree ferns into three natural alliances: *Sphaeropteris* Bernh. (with conform petiole scales; see Tryon, 1970, for definition of scale types); *Alsophila* sensu Tryon and *Nephelea* Tryon (with setate, marginate scales); and *Trichipteris* Presl, *Cyathea* Sm. sensu Tryon, and *Cnemidaria* Presl (with nonsetate, marginate scales). Based on this system, recent revisionary studies of the Cyatheaceae by Tryon (1971a, 1976), Gastony (1973), Stolze (1974), Windisch (1977, 1978), and Barrington (1978) have provided excellent data against which the present systematic conclusions have been compared.

Holttum (1961) divided the scaly tree ferns into two genera, *Cyathea* sensu lato and *Cnemidaria*. *Cnemidaria* sensu Holttum is equivalent to *Cnemidaria* sensu Tryon, whereas *Cyathea* sensu Holttum includes the rest of Tryon's scaly genera. *Cyathea* sensu lato was divided into subg. SPHAEROPTERIS (with setiferous (conform) petiole scales) and subg. ALSOPHILA (with flabelloid (marginate) scales). Subgenus ALSOPHILA included sects. ALSOPHILA (indusiate, axes greenish, fertile and sterile pinnules monomorphic) and GYMNOSPHAERA (exindusiate, axes dark, chocolate brown, fertile and sterile pinnules dimorphic) (Holttum, 1974).

The present genus *Alsophila* includes Tryon's *Alsophila* and *Nephelea* in the New World and Holttum's *Cyathea* subg. ALSOPHILA in the Old World. (All Old World species with marginate petiole scales also have setae. Species with nonsetate, marginate scales are restricted to the New World.) The extensive hybridization documented by Conant (1975, 1976) and Conant and Cooper-Driver (1980) is evidence that *Alsophila* sensu Tryon and *Nephelea* are more

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closely related than they are distinct and separable genera. Furthermore, Conant and Cooper-Driver (1980) have presented evidence that new species have arisen from these "intergeneric" hybrids. These species of hybrid origin can be assigned to a genus only on an arbitrary basis—i.e., whether genes for squaminate spines are inherited and expressed or not. Gastony (1973, 1974) has demonstrated that most species of *Alsophila* sensu Tryon and *Nephelea* have 16-spored sporangia, a feature that distinguishes them from other scaly Cyatheaceae. Gastony (1973) and Gastony and Tryon (1976) have shown that species of *Alsophila* sensu Tryon cannot be distinguished from *Nephelea* by their spores, lending additional support to their inclusion in the single genus *Alsophila.*

Species of *Alsophila* (in the present sense), however, are not known to hybridize with species of the nonsetate, marginate alliance (*Trichipteris, Cyathea* sensu stricto, *Cnemidaria*). The setate and nonsetate groups with marginate scales appear to be morphologically distinct and reproductively isolated from each other. Therefore, I cannot accept the conclusion of Holttum (1974) that these groups are elements of the single genus *Cyathea.*

This redefinition of *Alsophila* obviates the need for a reclassification of the family. Such a task is best left until there have been further biosystematic studies of the species with nonsetate, marginate scales and until the relationships of the species with marginate scales to those with conform scales are more fully understood.

DISTRIBUTION AND ECOLOGY

Alsophila is a genus of about 235 species distributed throughout the wet tropics of the Old and New Worlds. In the Old World, there are about 205 species divided between Africa and Madagascar (about 50 species—Schelpe, 1970; Holttum, 1981; Tardieu-Blot, 1951, 1953), the Indian subcontinent east to China and Japan (about 15 species—Holttum, 1965), Malaysia (about 114 species—Holttum, 1963), and Australasia and the Pacific (about 26 species—Holttum, 1964).

There are 30 species in the New World, of which 16 are centered in the Greater Antilles, 14 occur in Mexico and Central and South America, and 1 extends northward into the Lesser Antilles from Venezuela (see MAP 1). The center of diversity is in the Greater Antilles, where 16 species are endemic; Hispaniola, with 8 species and 5 endemics, is the island with the highest diversity.

The American species of *Alsophila* are mostly plants of the cloud forest–elfin forest type of habitat. Exceptions to this are *A. jimeneziana, A. cuspidata,* and *A. sternbergii,* which can often be found at lower elevations in gallery forest. *Alsophila* is primarily a genus consisting of understory, shade-loving species. Heliophilic plants like those found in the genera *Sphaeropteris, Trichipteris,* and *Cyathea* sensu Tryon are not found in American *Alsophila* and apparently do not occur in eastern Asian *Alsophila* either (Holttum, 1963).

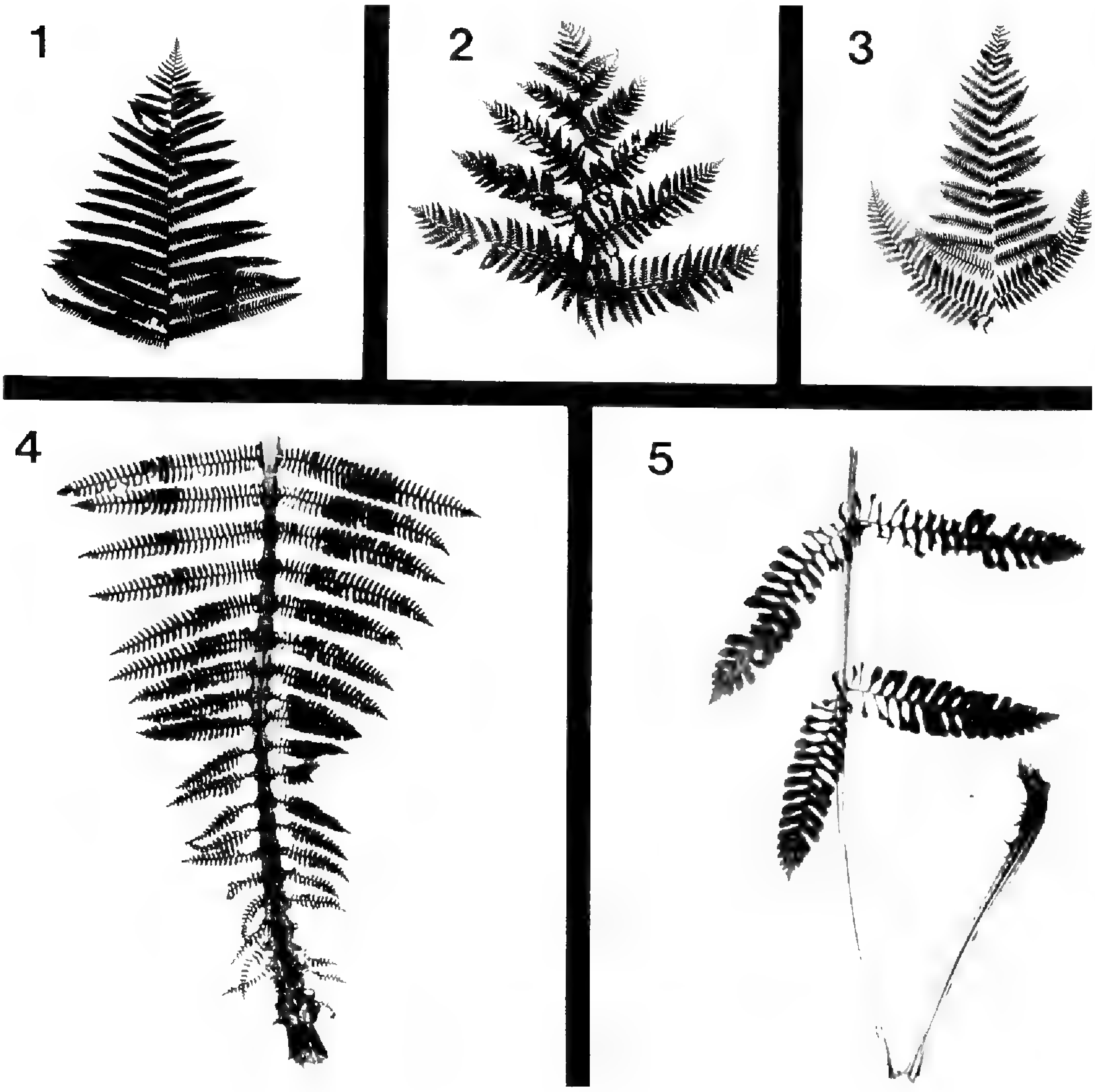
MORPHOLOGY

STEM. Stem habit and size provide good diagnostic characters for some species. In *Alsophila nockii* and *A. rupestris* the stem is short, prostrate, and less than

MAP 1. Distribution of the genus *Alsophila* in the Americas.

2 cm in diameter; in *A. brooksii* and *A. urbanii* it is short, prostrate (sometimes decumbent in *A. urbanii*), and to 6.5 cm in diameter. Among species with erect stems, most are greater than 6 cm in diameter and 2 m in length. Exceptions are *A. paucifolia*, which has an unusually slender (less than 2 cm in diameter) stem of unknown length, and *A. amintae* and *A. abbottii*, which generally have stems less than 5 cm in diameter and 1.5 m in length.

Squaminate spines may or may not be present on the stem. In general, spines are restricted to the species with tall, stout stems, although reduced spines are present in *Alsophila brooksii* and in certain hybrids between spiny and spineless species.



FIGURES 1–5. Lamina apices and bases: 1, *Alsophila bryophila* (*Conant 2265*), gradually tapering apex, × .08; 2, *A. woodwardioides* (*Conant 2028*), gradually tapering apex, × .09; 3, *A. cuspidata* (*Haught 2001*), imparapinnate apex, × .07; 4, *A. bryophila* (*Conant 2263*), gradually tapering base, × .18; 5, *A. urbanii* (*Conant 2102*), abruptly reduced base, × .18.

Adventitious buds occur in six of the nine species with squaminate spines in Mexico and Central and South America, as well as in *Alsophila woodwardioides,* of Jamaica, Hispaniola, and Cuba. *Alsophila sternbergii* is reported to produce stolons at the base of the stem that may facilitate vegetative reproduction in this species (Brade, 1971; as *Cyathea sampaioana*). Stolons are not known elsewhere among American species of the genus but are well documented (Hallé, 1966) in the African *A. manniana.*

The stem apices of all species are protected by deltoid to lanceolate scales with either a single apical seta or both apical and marginal setae.

LEAF. Although the petiole and the lamina are usually described separately, many of the characters of the petiole are present on the rachis in a reduced form, reminding us that the division of the leaf into petiole and lamina is arbitrary. This arbitrariness is also apparent in the treatment of aphlebiae and disjunct basal pinnae. Although these may more properly be parts of the lamina, they are treated here as belonging to the petiole.

The terminology for the parts of the fern leaf has been somewhat standardized (Tryon, 1960), but it is still confusing to compare fern species having complex (bipinnate-pinnatifid) leaves and those having simpler (pinnate-pinnatifid) ones. A factor contributing to the confusion is that some terms connote homologies whereas others relate more to size: petioles, rachises, pinna-rachises, pinnule-rachises, pinnae, and pinnules of bipinnate-pinnatifid and pinnate-pinnatifid leaves are homologous structures; costae, costules, and penultimate and ultimate segments are nonhomologous.

LAMINA. Lamina dissection varies from pinnate-pinnatifid to tripinnate (occasionally quadripinnate). Ten of the twelve species with pinnate-pinnatifid to bipinnate laminae occur in the Greater Antilles. *Alsophila rupestris* (Colombia) and *A. paucifolia* (Ecuador) also have the pinnate-pinnatifid architecture. Bipinnate-pinnatifid lamina dissection occurs in sixteen species distributed throughout the range of the genus in the Americas. Two species, *A. salvinii* (Mexico, Guatemala, Honduras) and *A. polystichoides* (Costa Rica and Panama), have tripinnate to quadripinnate laminae.

The lamina apex is one of two types. Most species have an acuminate apex in which the more distal pinnae are gradually reduced (FIGURES 1, 2). Nine species from Mexico, Central and South America, and the Lesser Antilles have a distinctly pinnalike imparapinnate lamina apex (FIGURE 3).

The lamina may be gradually narrowed at the base as in *Alsophila amintae* and mature leaves of *A. bryophila* (FIGURE 4) or abruptly reduced as in *A. urbanii* (FIGURE 5). Some species (e.g., *A. portoricensis*) are variable with respect to the lamina base.

Pinna shape is often a useful character. A measure of pinna shape is width divided by length: long, narrow pinnae will have low width/length quotients; broader ones will have higher quotients.

PETIOLE. Petiole length is generally correlated with lamina base. Species with gradually narrowed lamina bases are usually short petiolate, whereas those with abruptly reduced lamina bases tend to be long petiolate.

Squaminate spines may or may not be present on the petiole. The presence of petiole spines is precisely correlated with the presence of stem spines. Reduced petiole spines may be present in *Alsophila brooksii* and on certain hybrids between spiny and nonspiny species.

Tardieu-Blot (1941) found that the aphlebioid[1] species of Madagascar were of three basic types. The first, including *Alsophila decrescens* (Kuhn) Tryon (as *Cyathea decrescens*), has gradually tapering lamina bases in which pinnae grade into basal subaphlebioid pinnae. American species belonging to this group include *A. amintae, A. abbottii, A. minor, A. auneae, A. grevilleana,* and *A. setosa.* (In *A. minor* the basal subaphlebioid pinnae may be disjunct.) The

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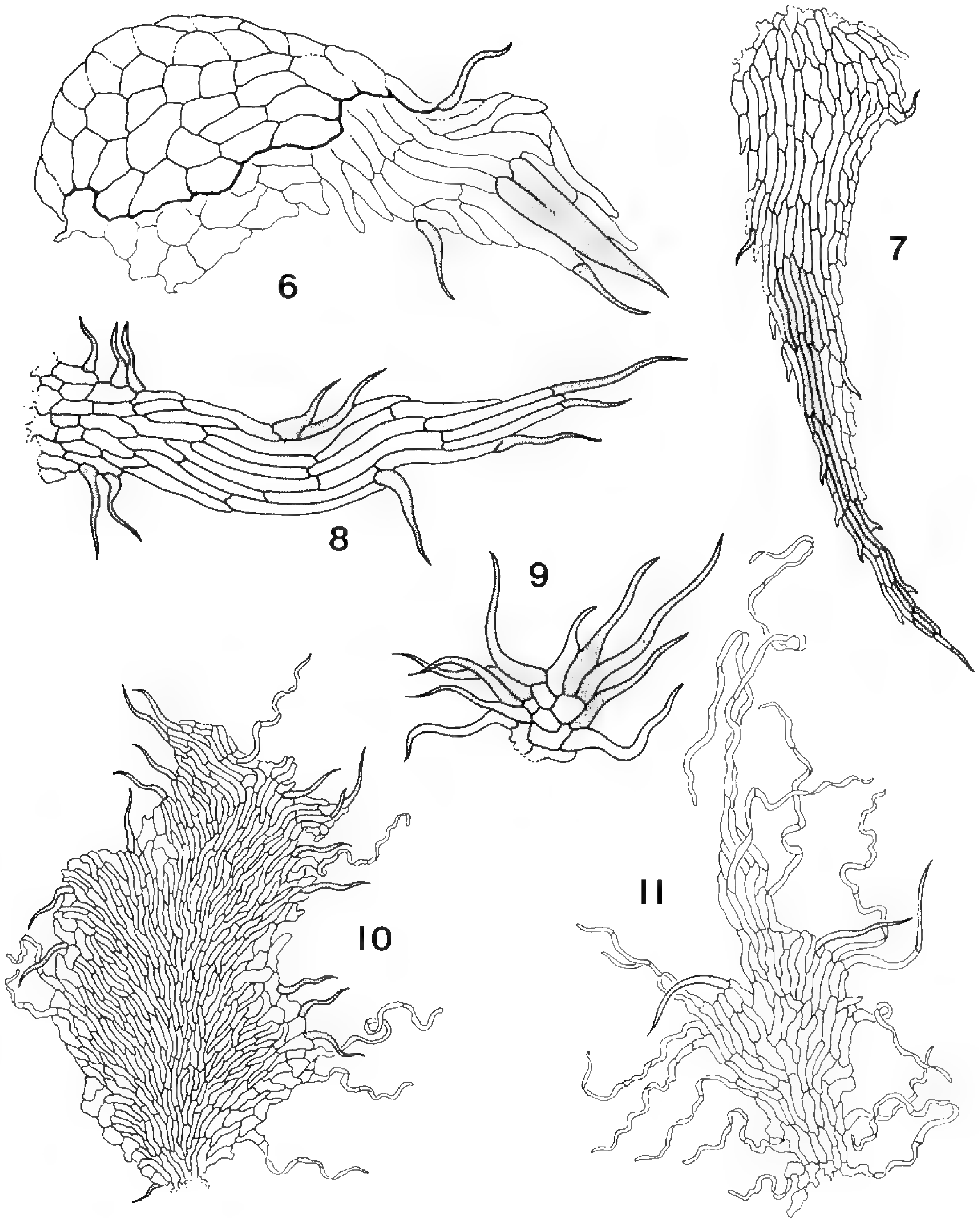
[1] Although the terms aphlebiae and aphlebioid may be technically incorrect, as suggested by Holttum (1981), they are maintained here because these terms have historically been consistently used in describing skeletonized basal pinnae.



FIGURES 6–11. Lamina scales. 6, 7, *Alsophila nockii:* 6, *Hart 13,* bullate scale, × 100; 7, *Underwood 1355,* bicolorous, lanceolate scale with single apical seta, × 65. 8, *A. brooksii* (*Conant 677*), lanceolate scale with marginal and apical setae, × 68. 9, *A. salvinii* (*Stone & Broome 2814*), acaroid scale, × 105. 10, 11, *A. engelii* (*Pennell 9695*): 10, setate, flabellate scale, × 28; 11, highly dissected scale, × 50.

second type, including *A. dregei* (Kunze) Tryon (as *C. dregei*), has nonaphlebioid basal pinnae that are separated from the rest of the pinnae by a large gap. Although *A. bryophila* has disjunct basal pinnae of this type in some juvenile plants, its pinnae are pinnatifid and those of *A. dregei* are pinnate-pinnatifid. The third type, including *A. boivinii* Ettingsh., has highly skeletonized aphlebiae that are separated from the rest of the pinnae by a gap. Three species, *A. capensis, A. salvinii,* and *A. urbanii,* have aphlebiae of this type.

INDUMENT. The abaxial surface of the axes and veins of the lamina are invested with various kinds of scales, squamules, trichomes, and trichomidia that are of considerable taxonomic importance. The indument on the adaxial surface of the axes and veins is more or less similar in all species and is therefore usually not described.

Bullate scales (FIGURE 6) are nearly orbicular to elongate, inflated, and with or without setae. If they are nearly flat, they are termed "subbullate." Bullate scales are present on the costae or costules of 14 of 16 species in the Greater Antilles (all except *Alsophila brooksii* and *A. urbanii*) and of 4 (*A. salvinii, A. tryoniana, A. engelii,* and *A. capensis*) of 14 continental species.

Bicolorous (dark bodied, light margined), lanceolate scales with a single apical seta (FIGURE 7) (or sometimes with a few setae at the base) are found in four related species of the Greater Antilles: *Alsophila amintae, A. abbottii, A. nockii,* and *A. tussacii. Alsophila imrayana,* of South America and the Lesser Antilles, has often concolorous, lanceolate scales with a single apical seta. *Alsophila paucifolia,* of Ecuador, has bicolorous scales with a very dark, indurated body and a single apical seta; however, these tend to be deltoid in shape. *Alsophila woodwardioides, A. salvinii,* and *A. capensis* have bicolorous, lanceolate scales with one to several apical setae.

Concolorous to bicolorous, elongate to lanceolate scales with marginal and apical setae (FIGURE 8) are found in many species. In the Greater Antilles they are present in *Alsophila hotteana, A. minor, A. brooksii, A. urbanii,* and *A. portoricensis.* Four continental species, *A. tryoniana, A. polystichoides, A. sternbergii,* and *A. firma,* also have this type of scale.

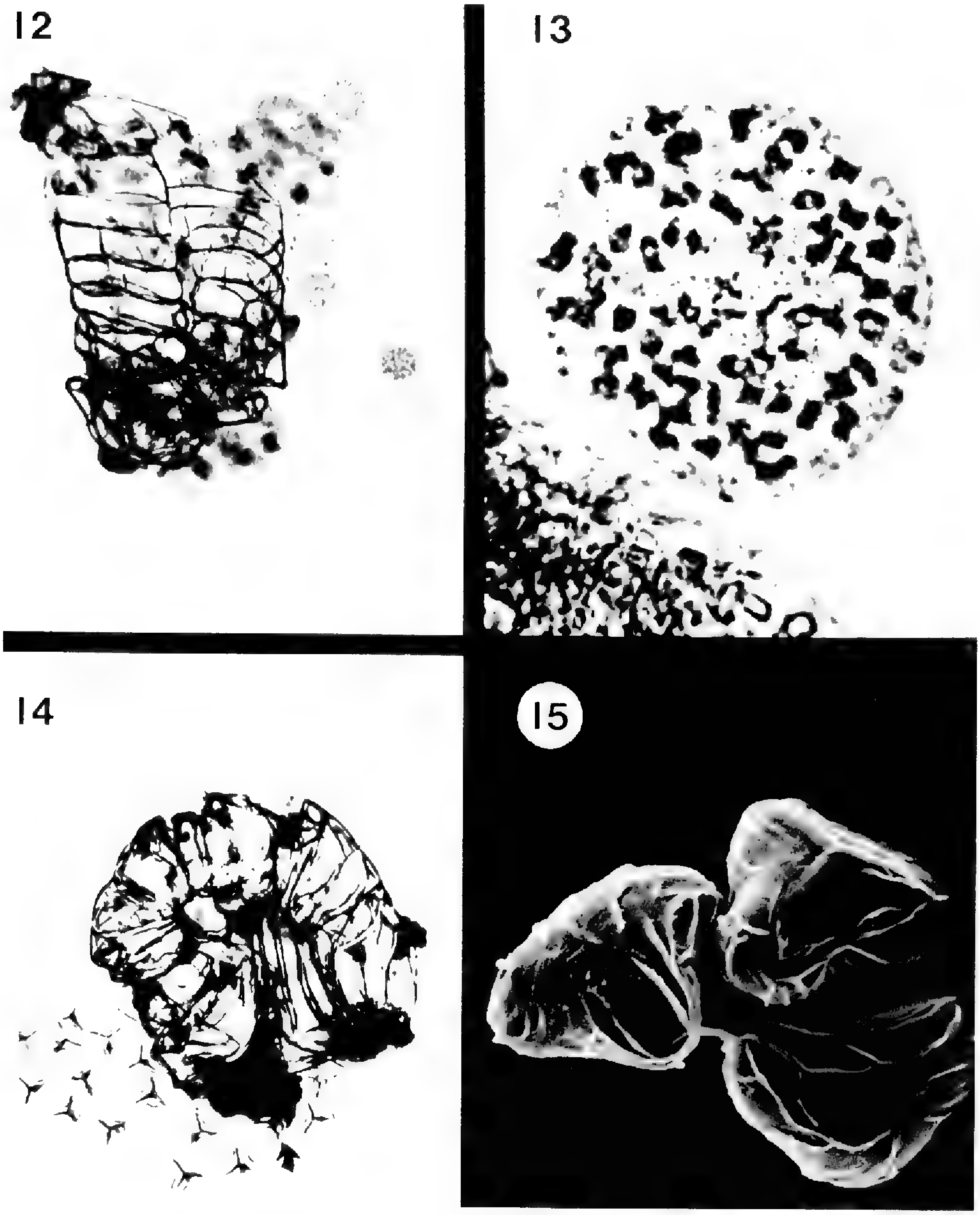
Acaroid scales (FIGURE 9) are small and orbicular, usually with an indurated body and many dark, marginal setae; they may be reduced to tiny, setate squamules nearly without a scale body. Species in the Greater Antilles with acaroid scales include *Alsophila hotteana, A. minor, A. brooksii, A. balanocarpa, A. urbanii,* and *A. portoricensis.* Among continental species, such scales occur in *A. salvinii, A. setosa, A. sternbergii, A. cuspidata,* and *A. erinacea.*

Alsophila engelii, of Colombia and Venezuela, has two additional scale types not found in other American species of the genus. One is flabellate and setate (FIGURE 10) (this type may be reduced to tiny, setate squamules with unsclerified bodies). The second is highly dissected and setate (FIGURE 11), giving an axis the appearance of being pubescent.

Young axes may be densely deciduously scurfy with tiny, appressed squamules; this character was not found to be of taxonomic significance, however.

Most species of *Alsophila* have trichomes on the abaxial surface of their smaller axes. *Alsophila bryophila* and *A. auneae* are characterized by a particularly dense pubescence, while *A. amintae, A. nockii, A. paucifolia, A. salvinii,* and *A. capensis* lack trichomes on their axes. *Alsophila cuspidata* and *A. sternbergii* have stellate trichomes on their veins in addition to unbranched ones on their larger axes.

Tiny, antrorse trichomidia may or may not be present on the abaxial surface



FIGURES 12–15. Chromosomes and spores of *Alsophila amintae*. 12–14, *Conant & Kitfield 2274*: 12, sporangium with 4 spore mother cells, × 200; 13, spore mother cell in diakinesis showing n = ca. 69 pairs, × 1850; 14, sporangium with 16 spores (arrow indicates spore partially obscured by sporangium), × 200. 15, *Conant 595*, spores, × 1500.

of the veins. These are usually golden in color, but in *Alsophila engelii* they are whitish.

SORI. The sori are exindusiate or with a hemitelioid (FIGURE 48), meniscoid (FIGURE 25), cyatheoid (FIGURE 18), or sphaeropteroid (FIGURE 38) indusium. Sporangia are clustered about a usually columnar receptacle, resulting in a semiglobose to nearly globose sorus. They have an oblique annulus and a short stalk that meets the capsule to one side of the basalmost portion of the annulus. Gastony (1973, 1974) has shown that the archesporial cell typically divides twice mitotically, producing 4 spore mother cells (FIGURE 12), and that each of these undergoes meiosis (FIGURE 13), producing a total of 16 spores per sporangium (FIGURE 14). Gastony and Tryon (1976) reported several species of *Alsophila* (including the American *A. salvinii* and *A. capensis*) with 64-spored sporangia. Spores of *Alsophila* are trilete and have a reticulate pattern of ridges (FIGURE 15) (Gastony, 1973, 1974; Conant, 1975; Gastony & Tryon, 1976; Conant & Cooper-Driver, 1980).

CYTOLOGY

Chromosome counts in the genus *Alsophila* have been $n = 69$ or $n =$ ca. 69 pairs of bivalents. Brownlie (1958, 1965) reported $n = 69$ for four species from Australasia: *A. alata* Fourn., *A. colensoi* Hooker, *A. smithii* (Hooker) Tryon, and *A. tricolor* (Colenso) Tryon (all as species of *Cyathea*).

From the areas of India and Sri Lanka, Manton and Sledge (1954), Mehra and Singh (1955), and Ghatak (1962) have reported $n = 69$ or ca. 69 for eight species: *Alsophila gigantea* Hooker, *A. hookeri* (Thwaites) Tryon, *A. khasiana* Kuhn, *A. latebrosa* Hooker, *A. ornata* Bedd., *A. sinuata* (Hooker & Grev.) Tryon, *A. spinulosa* (Hooker) Tryon, and *A. walkerae* (Hooker) J. Sm. (all as species of *Cyathea*).

Manton (1954) cited $n = 69$ for *Alsophila latebrosa* (as *Cyathea latebrosa*), from Malaysia. Roy and Holttum (1965) cited $n =$ ca. 69 for *A. podophylla* Hooker (as *Cyathea podophylla*), from southern China. Manton and Sledge (1954) reported $n = 70$ for *A. capensis* (L. f.) J. Sm., and Manton (1959) reported $n =$ ca. 69 for *A. camerooniana* (Hooker) Tryon (both from Africa and both as species of *Cyathea*). The report of $n = 70$ for *A. capensis* was from a single plant at Kew Gardens. Since other species in the family have $n = 69$, cytological reexamination of this species in the field is desirable.

Walker (1966) reported $n = 69$ for three Jamaican species, *Alsophila auneae, A. grevilleana,* and *A. tussacii* (all as species of *Cyathea*). Gomez-Pignataro (1971) reported $n = 69$ for two Costa Rican species, *A. erinacea* and *A. firma* (both as species of *Cyathea*). Conant (1976) and Conant and Cooper-Driver (1980) cited $n =$ ca. 69 for *A. amintae, A. bryophila, A. amintae* × *A. portoricensis,* and *A. bryophila* × *A. portoricensis,* all from Puerto Rico.

Perhaps the most unusual aspect of the cytology of the genus *Alsophila* is that the two hybrids that have been examined are fertile diploids. Spores are well formed and germinate readily when sown on a nutrient agar medium.

SPECIATION

The genus *Alsophila* apparently originated in the Old World, where 87 percent of the known taxa are found. The American species of *Alsophila* are most closely related to the African and Madagascan elements of the genus (Holttum, 1981), and the presence of *Alsophila* in the New World is undoubtedly the result of long-distance dispersal from the east. Dust from the Sahara Desert encountered by aerobiologists sampling air in the Caribbean provides evidence that wind patterns favor such long-distance dispersal (Prospero, 1968; Prospero *et al.*, 1970).

At least four separate migrations are believed to have established the basic geographic elements of American *Alsophila*. In some cases migration may have been recent, resulting in little morphological differentiation of the immigrant. Thus, *A. capensis* in southeastern Brazil is only slightly different from that species in southern Africa and was assigned subspecific rank in accordance with the degree of differentiation. *Alsophila salvinii*, of Mexico, Guatemala, and Honduras, is a distinct American species clearly related to species of Holttum's sect. GYMNOSPHAERA (Holttum, 1974, 1981), of Madagascar and Borneo.

In other cases, migrations may have occurred in the more distant past, allowing time for more morphological differentiation and resulting in new American species groups. It is more difficult to determine the relations between American and Old World species groups than it is to relate the above two American taxa to their Old World relatives. This may be a direct result of the diversification process. Although a few characters may still be held in common, shifts in gene frequencies result in a situation where characters that are obscure in the Old World group may become common and predominant in the New World group. Such may have been the case with the development of the squaminate spine in the New World.

Holttum (1981) suggests there are about 20 species with complex leaves and squaminate spines (excluding *Alsophila setosa*, as *Cyathea setosa*) that form a closely allied group. Gastony (1973) recognized only 15 such species (all as *Nephelea*, and with one suggested as a probable hybrid) and clearly demonstrated that they fall into two distinct groups, which are referred to below as the *A. cuspidata* and the *A. woodwardioides* groups.

The South American species with imparapinnate lamina apices, ovate to elliptic pinnae (width/length quotient (0.23–)0.27–0.31), and sphaeropteroid indusia include *Alsophila cuspidata*, *A. sternbergii*, *A. erinacea*, *A. incana*, *A. imrayana*, and *A. firma* and are hereafter referred to as the *A. cuspidata* group. This appears to be related to the *A. serratifolia* group of Madagascar, which includes *A. serratifolia* (Baker) Tryon, *A. marattioides* (Kaulf.) Tryon, *A. perrieriana* (C. Chr.) Tryon, and *A. tsilotsilensis* (Tardieu-Blot) Tryon (all as species of *Cyathea*) (Tardieu-Blot, 1951) and is characterized by the imparapinnate lamina apex, a similar pinna size and shape, and (usually) a sphaeropteroid indusium. In the *A. cuspidata* group the lamina is slightly more complex (bipinnate-pinnatifid) and the petioles and stems are armed with conspicuous squaminate spines, whereas in the *A. serratifolia* group the lamina is bipinnate and the spines are inconspicuous or absent.

The Greater Antillean species with a gradually tapering lamina apex, long, narrow pinnae (width/length quotient 0.12–0.17(–0.24)), and pinnate-pinnatifid to bipinnate lamina dissection (including *Alsophila minor*, *A. bryophila*, *A. hotteana*, *A. amintae*, *A. abbottii*, *A. nockii*, *A. brooksii*, and *A. urbanii*) are hereafter referred to as the *A. minor* group. Holttum (1981) comments that these Antillean species appear to be related to the group of African and Madagascan species (here referred to as the *A. decrescens* group) with a similar lamina apex, pinna shape, and lamina dissection. African species include *A. mossambicensis* (Baker) Tryon, *A. camerooniana* (Hooker) Tryon, and *A. welwitschii* (Hooker) Tryon (all as species of *Cyathea*). Madagascan species with these characters, too numerous to list in their entirety, include *A. madagascarica* Bonap., *A. approximata* (Bonap.) Tryon, *A. zakamenensis* (Tardieu-Blot) Tryon, and *A. decrescens* (Kuhn) Tryon (Tardieu-Blot, 1951; all as species of *Cyathea*). In the *A. minor* group the cyatheoid indusium is predominant, whereas in the *A. decrescens* group the sphaeropteroid indusium is more common among Madagascan species. Both the *A. minor* and the *A. decrescens* groups include several species with aphlebioid to subaphlebioid basal pinnae; *A. urbanii* and *A. zakamenensis* are notably similar in this respect.

Once established, the South American element may have diversified to some extent, forming some or most of the species in the *Alsophila cuspidata* group. The sequence of species from southeastern Brazil north through the Andes to Mexico suggests that a process such as evolutionary migration (Tryon, 1971a, 1971b) may have been involved in forming this species group. Similarly, the Greater Antillean immigrant may have undergone some adaptive radiation, as frequently occurs in island archipelagoes, forming some or most of the species in the *A. minor* group. These geographic processes, however, are thought to account for only half to two-thirds of the species diversity within present-day American *Alsophila*. The remainder is believed to have arisen via allohomoploid speciation. Conant and Cooper-Driver (1980) have discussed the origins via allohomoploidy of *A. setosa, A. tryoniana, A. polystichoides, A. balanocarpa,* and *A. auneae* (as species of *Nephelea*). The six Greater Antillean species with bipinnate-pinnatifid leaf architecture, spines, a gradually tapering lamina apex, and bullate scales (*A. woodwardioides, A. jimeneziana, A. fulgens, A. grevilleana, A. portoricensis,* and *A. tussacii*; hereafter referred to as the *A. woodwardioides* group) are interesting to consider in relation to the allohomoploid pathway. Gastony (1973) viewed them as perhaps being derived via divergent geographic speciation from an ancestral plexus similar to the spiny, pinnate-pinnatifid *A. auneae* and *A. balanocarpa* (as *Nephelea pubescens* and *N. balanocarpa*), which presumably were related to the *A. minor* group. *Alsophila tryoniana,* the only spiny continental species with bipinnate-pinnatifid leaf architecture, a gradually tapering lamina apex, and bullate scales, was interpreted as being related to the Antillean *A. woodwardioides* group, and as perhaps being intermediate between the Antillean and the continental *A. cuspidata* groups. Conant and Cooper-Driver (1980) have proposed a different origin for *A. tryoniana* (as *Nephelea tryoniana*), suggesting that the gradually tapering lamina apex and the bullate scales were inherited from *A. salvinii* via allohomoploid speciation.

Reappraisal of the *Alsophila woodwardioides* group in view of the allohomoploid pathway results in an interpretation different from that of Gastony (1973). The numerous instances of hybridization between the *A. minor* and the *A. woodwardioides* groups (Conant, 1975, 1976; Conant & Cooper-Driver, 1980) and the extent to which they share unusual characters indicate an intimate, reticulate relationship of the groups. Characters such as the pubescent indusium in *A. minor, A. brooksii,* and *A. portoricensis,* the bicolorous, lanceolate laminar scales with a single apical seta in *A. abbottii, A. amintae, A. nockii,* and *A. tussacii,* and the subaphlebioid basal pinnae in *A. amintae, A. abbottii, A. minor,* and *A. grevilleana* result in a reticulate pattern of species relationships. The only significant differences between the *A. minor* and the *A. woodwardioides* groups are that members of the former tend to be pinnate-pinnatifid and spineless whereas those of the latter are bipinnate-pinnatifid and spiny. The origin of the latter two characters may have been in the *A. cuspidata* group. Migration of a member of this South American group into the Greater Antilles, subsequent hybridization with a member or members of the *A. minor* group, and later allohomoploid speciation could account for the bipinnate-pinnatifid leaf architecture, the spines, and the gradually tapering lamina apex of the *A. woodwardioides* group. This would also explain the sphaeropteroid indusium in *A. fulgens* and the adventitious buds in *A. woodwardioides,* characters otherwise restricted to continental species of the *A. cuspidata* group. Following introduction of Andean characters into the Greater Antilles, allohomoploid speciation could account for all species of the *A. woodwardioides* group and for *A. auneae* and *A. balanocarpa.*

HYBRIDS

Hybrids in the genus *Alsophila* can be divided into two groups. The first comprises species of hybrid origin in which reproduction has been stabilized by allohomoploidy. Conant and Cooper-Driver (1980) have discussed the origins of *A. auneae, A. balanocarpa, A. tryoniana, A. polystichoides,* and *A. setosa* (as species of *Nephelea*), dealt with above in the section on Speciation. Holttum (1981) also suggests that *A. setosa* is the result of hybridization between *A. capensis* and *A. sternbergii* (all as species of *Cyathea*).

The second group consists of hybrids that are not reproductively stable or are too poorly known to be admitted to specific status. Diagnoses of these follow the enumeration of species in the Systematic Treatment. Comments below pertain to this latter group.

The detection of hybrids has been facilitated by the presence of certain morphological markers. Lamina dissection, pinna shape, and presence of squaminate spines have been particularly useful. In the Greater Antilles six species (the *Alsophila woodwardioides* group) have bipinnate-pinnatifid laminae, ovate to elliptic pinnae (width/length quotient 0.29 or more), and long, squaminate spines. Eight species (the *A. minor* group) have pinnate-pinnatifid to bipinnate laminae, long, narrow pinnae (width/length quotient 0.17 or less, except 0.24 or less in *A. urbanii*) and are without spines. Crosses between the two groups can be recognized in the field by the combination of a bipinnate-lobed to bipinnate-pinnatifid lamina dissection with a longer and narrower (width/length quotient 0.17–0.29) pinna shape than is normally encountered in the more complex leaves. Plants with this intermediate lamina also usually have short spines, an intermediate condition in a cross between long-spined and spineless species. Crosses within groups are difficult to recognize and have been detected only by intensive field or herbarium study.

Field observations have been made on six of the nine hybrids listed at the end of the Systematic Treatment. All were growing in or near ecologically disturbed areas. In some cases the disturbances were due to the activities of man, such as road building or the clearing of land for agricultural purposes. Three of the hybrids were found along the upper reaches of streams remote from any disturbance by man, and two were encountered numerous times in apparently virgin cloud forest. Small landslips are common along stream banks and in the water-soaked soil of the cloud forest; such disturbances provide places where natural hybridizations can occur.

It is difficult to determine whether the hybrid plants encountered in the field are F_1 or later-generation hybrids. Some tend to be rare and intermediate in morphology, suggesting they are the first generation. Others are very close to one parent or the other, indicating either a backcross or F_2 segregate origin. Conant and Cooper-Driver (1980) have demonstrated that *Alsophila amintae* × *A. portoricensis* (as *A. dryopteroides* × *Nephelea portoricensis*) is more abundant than either of its parents in one population and appears to be reproducing itself. These later-generation plants are morphologically uniform (see *fig. 2* in Conant & Cooper-Driver, 1980), suggesting that this hybrid may be an incipient allohomoploid species. Recognition at specific rank, however, will await laboratory analysis of its reproductive stability.

HERBARIA

In addition to the herbaria listed in Lanjouw and Stafleu (1964) and cited by the recommended abbreviations, the following are also mentioned: herbarium of the El Verde Field Station of the Center for Energy and Environmental Research, Río Piedras, Puerto Rico (Herb. EVFS), and the herbarium of the Jardín Botánico Rafael M. Moscoso, in Santo Domingo, Dominican Republic (Herb. JBRMM).

SYSTEMATIC TREATMENT

Alsophila R. Br. Prodr. Fl. Novae Holland. 158. 1810. TYPE: *Alsophila australis* R. Br.

Gymnosphaera Blume, Enum. Pl. Javae, 242. 1828. TYPE: *Gymnosphaera glabra* Blume = *Alsophila glabra* (Blume) Hooker.

Amphicosmia Gardner, London J. Bot. **1:** 441. 1842. LECTOTYPE: *Amphicosmia riparia* (Willd.) Gardner (*Cyathea riparia* Willd.) = *Alsophila capensis* (L. f.) J. Sm. (for lectotypification, see R. M. Tryon, Contr. Gray Herb. **200:** 25. 1970.)

Dichorexia Presl, Gefässbündel Stipes der Farrn, 36. 1847 (preprint from Abhandl. Königl. Böhm. Ges. Wiss. V. **5:** 344. 1848). TYPE: *Dichorexia latebrosa* (Hooker) Presl = *Alsophila latebrosa* Hooker.

Thysanobotrya Alderw. Bull. Jard. Bot. Buitenzorg, II. **28:** 66. 1918. TYPE: *Thysanobotrya arfakensis* (Gepp) Alderw. (*Polybotrya arfakensis* Gepp) = *Alsophila biformis* Rosenstock.

Nephelea Tryon, Contr. Gray Herb. **200:** 37. 1970. TYPE: *Nephelea polystichoides* (Christ) Tryon = *Alsophila polystichoides* Christ.

Stem prostrate, decumbent, or erect, to 15 m tall and 15 cm in diameter (excluding adventitious roots), with or without squaminate spines. Leaves to 4.4 by 1.6 m, exstipitate to long-petiolate; petiole brown to black, smooth to tuberculate or with squaminate spines, the base with uniformly tan to bicolorous, deltoid to lanceolate, marginate scales (these fleshy in 1 species) having single (usually dark) apical seta or both apical and marginal setae, with or without aphlebiae or subaphlebioid basal pinnae, occasionally with gap between basal aphlebiae, subaphlebioid basal pinnae, or basal pinnae and next higher pinna pair; lamina pinnate-pinnatifid to rarely quadripinnate, the base gradually tapering or abruptly narrowed, the apex gradually tapering and acute to acuminate or abruptly reduced and imparapinnate, the rachis stramineous to black, invested with various combinations of trichomes, squamules, and/or scales, or glabrous; pinnae sessile to stalked, narrower to broader at base, apex blunt tipped to attenuate, the pinna-rachis with various combinations of trichomes, scales, and/or squamules, the veins free, 6 to 24 pairs, often with tiny, antrorse, golden trichomidia beneath; indusia lacking or hemiteloid, meniscoid, cyatheoid, or sphaeropteroid, glabrous or pubescent; sporangia with oblique annulus uninterrupted by stalk, usually with 16 trilete spores. (Description applies especially to American elements of genus; all variations of nondiagnostic characters of Old World species not included.)

USE OF THE KEY

The following is a key to complete and mature specimens; it includes characters of the lamina apex, middle pinnae, petiole, and basal pinnae, as well as data on size, posture, and armament of the stem, provenance, and ecology. Incomplete specimens can be identified if one has some knowledge of the geography of certain character combinations discussed above in the sections on Morphology and Speciation. Juvenile specimens may be problematic. For example, young plants of *Alsophila bryophila* and *A. minor* may have a conspicuous gap between the basal one to three pairs of pinnae or subaphlebioid pinnae and the main portion of the lamina. If the disjunct basal pinnae are reduced or lost, specimens often appear to have a long petiole, which may cause confusion at couplet 3 in the key.

The descriptions of lamina complexity apply to the mid-portions of the middle pinnae. The user should beware of specimens from the Greater Antilles that are bipinnate-lobed to bipinnate-pinnatifid and have long, narrow pinnae (width/length quotient 0.17–0.29). These may be hybrids and are discussed above in the section entitled Hybrids. They are enumerated at the end of the Systematic Treatment (nos. 31–39).

Descriptions of indument and scales apply to the abaxial surface of axes.

KEY TO SPECIES OF ALSOPHILA

1. Stem and petiole without conspicuous squaminate spines (reduced spines occasionally present in *A. brooksii*).
    2. Lamina pinnate-pinnatifid to bipinnate; stem prostrate, decumbent, or erect.

3. Lamina sessile to short-petiolate, gradually narrowed at base (abruptly narrowed in *A. rupestris*).

4. Indusia cyatheoid.

5. Large, erect plants; stem always more than 2.5 cm in diameter.

6. Indusia glabrous; stem less than 6 cm in diameter, less than 2 m tall; scales of pinna-rachis and costule mostly without lateral setae.

7. Pinna-rachis sparsely to moderately pubescent; basal pinnules often completely overlapping and clasping rachis; petiole and rachis tan to brown. [Hispaniola]. .... 3. *A. abbottii.*

7. Pinna-rachis glabrous; basal pinnules not or only partly overlapping rachis; petiole and rachis dark purplish-brown. [Puerto Rico]. .... 2. *A. amintae.*

6. Indusia pubescent; stem to 11 cm in diameter and 7 m tall; scales of pinna-rachis and costule with many conspicuous lateral setae. [Hispaniola, Cuba]. .... 6. *A. minor.*

5. Small, prostrate plants; stem never more than 2.5 cm in diameter.

8. Petiole and rachis black; pinna-rachis with trichomes only. [Colombia]. .... 9. *A. rupestris.*

8. Petiole brown; rachis stramineous; pinna-rachis with whitish to bicolorous, lanceolate scales with single apical seta, and with trichomes and bullate scales. [Jamaica]. .... 1. *A. nockii.*

4. Indusia meniscoid.

9. Pinna-rachis densely pubescent and with few nonsetate to setate, whitish, bullate scales; petiole and rachis purplish-brown. [Puerto Rico]. .... 5. *A. bryophila.*

9. Pinna-rachis sparsely to moderately pubescent and with acaroid scales and dark, ovate scales with apical and lateral setae; petiole brown; rachis tan. [Haiti]. .... 4. *A. hotteana.*

3. Lamina long-petiolate, abruptly narrowed at base.

10. Pinnules less than 5 mm wide; petiole never with aphlebiae.

11. Indusia sphaeropteroid, variously rupturing at maturity, glabrous; petiole and rachis black; stem erect. [Ecuador]. .. 10. *A. paucifolia.*

11. Indusia cyatheoid, intact at maturity, pubescent; petiole and rachis brown to stramineous; stem prostrate. [Puerto Rico, Hispaniola, Cuba]. .... 7. *A. brooksii.*

10. Pinnules more than 5 mm wide; indusia cyatheoid, occasionally with 1 or 2 clefts, glabrous (occasionally slightly pubescent); petiole with or without aphlebiae at base; stem prostrate to decumbent. [Dominican Republic]. .... 8. *A. urbanii.*

2. Lamina bipinnate-pinnatifid to tripinnate (rarely quadripinnate); stem erect.

12. Sorus indusiate; lamina bipinnate-pinnatifid; petiole and rachis tan to brown.

13. Indusia hemitelioid; petiole with 1 to few pairs of aphlebiae at base; middle pinnae with width/length quotient ca. 0.36. [SE Brazil]. .... 13. *A. capensis.*

13. Indusia deeply cyatheoid to sphaeropteroid; petiole without aphlebiae; middle pinnae with width/length quotient ca. 0.27. [Colombia, Venezuela]. .... 11. *A. engelii.*

12. Sorus exindusiate; lamina tripinnate (rarely quadripinnate); petiole and rachis shiny black; petiole with several pairs of aphlebiae. [Mexico, Guatemala, Honduras]. .... 12. *A. salvinii.*

1. Stem and petiole with conspicuous squaminate spines.

14. Lamina pinnate-pinnatifid to bipinnate.

15. Pinnules sessile and often basally auriculate; basal pinnae reduced but not

subaphlebioid; middle pinnae with width/length quotient ca. 0.19. [Cuba]. .... 15. *A. balanocarpa.*

15\. Pinnules adnate and without basal auricles; basal pinnae reduced and often subaphlebioid; middle pinnae with width/length quotient ca. 0.12. [Jamaica]. .... 14. *A. auneae.*

14\. Lamina bipinnate-pinnatifid to tripinnate (rarely quadripinnate).

16\. Lamina apex gradually tapering. [Greater Antilles, except *A. tryoniana*].

17\. Sorus indusiate; scales and trichomes of costae and costules various.

18\. Indusia meniscoid to deeply cyatheoid, glabrous or pubescent; leaf tissue papyraceous to subcoriaceous.

19\. Veins and indusia glabrous.

20\. Basal pinnae reduced or not, not subaphlebioid; scales and trichomes of costae various.

21\. Costa usually sparsely squamose, the scales brown to blackish and with apical and lateral setae.

22\. Pinna-rachis usually narrowly alate distally, the wings green; costa glabrous to sparsely pubescent; stem spines less than 5 mm long. [Hispaniola]. .... 17. *A. jimeneziana.*

22\. Pinna-rachis not alate distally; costa pubescent, often densely so; stem spines to 15 mm long. [Jamaica, Hispaniola, Cuba]. .... 20. *A. woodwardioides.*

21\. Costa usually densely squamose, the scales tan to bicolorous and with a single apical seta. [Jamaica]. .... 21. *A. tussacii.*

20\. Basal pinnae often highly reduced and subaphlebioid; costa squamose to furfuraceous and with dark-setate, bullate scales; pinna-rachis usually narrowly alate distally, with wings green. [Jamaica]. .... 16. *A. grevilleana.*

19\. Veins and indusia pubescent. [Puerto Rico]. .... 19. *A. portoricensis.*

18\. Indusia sphaeropteroid, glabrous; leaf tissue coriaceous. [Hispaniola]. .... 18. *A. fulgens.*

17\. Sorus exindusiate; costules sparsely pubescent and with bullate to subbullate scales. [Guatemala, Nicaragua, Honduras]. . 23. *A. tryoniana.*

16\. Lamina imparapinnate. [Mexico, Central and South America, Lesser Antilles].

23\. Indusia meniscoid to sphaeropteroid; basal pinnae not subaphlebioid.

24\. Lamina bipinnate-pinnatifid; indumentum of veins various; indusia various; width/length quotient of middle pinnae 0.23–0.32.

25\. Veins with whitish, stellate trichomes or minute, white, stellate squamules.

26\. Leaf tissue papyraceous; veins with white, stellate trichomes; petiole scales with apical setae and with or without lateral setae. [Below 1200 m alt.].

27\. Veins and indusia with stellate trichomes having 3 or 4 more or less straight (sometimes dark) arms; indusia firm, brown, persistent, mostly subsphaeropteroid. [Nicaragua, Costa Rica, Panama, Colombia, French Guiana, Ecuador, Amazonian Brazil, Peru, Bolivia, Paraguay]. .... 26. *A. cuspidata.*

27\. Veins and indusia with stellate trichomes having irregular arms; indusia firm, brown, and persistent (or indument of indusia and veins less conspicuous and indusia fugacious). [Brazil, Paraguay]. .... 27. *A. sternbergii.*

26. Leaf tissue coriaceous; veins with occasional minute, white, stellate squamules; indusia glabrous to squamulate; petiole scales with single apical seta. [700–2800 m alt.; Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia]. .... 24. *A. erinacea.*

25. Veins mostly without trichomes or with unbranched trichomes or with squamules not white or stellate.
    28. Indusia subsphaeropteroid to sphaeropteroid, glabrous or with few minute squamules; petiole spines to 14 mm.
        29. Petiole scales with single apical seta; basal pinnae not reduced; middle pinnae with width/length quotient ca. 0.30; pinna rachis not alate distally. [Costa Rica, Panama, Venezuela, Lesser Antilles, Colombia, Ecuador]. .... 25. *A. imrayana.*
        29. Petiole scales with apical and numerous lateral setae; basal pinnae reduced; middle pinnae with width/length quotient ca. 0.23; pinna-rachis usually alate distally, with wings green. [Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Panama, Ecuador]. .... 29. *A. firma.*
    28. Indusia meniscoid, cyatheoid, or subsphaeropteroid, the latter type pubescent; petiole scales with single apical seta; petiole spines to 4 mm. [Colombia, Ecuador, Peru, Bolivia, Argentina]. .... 28. *A. incana.*

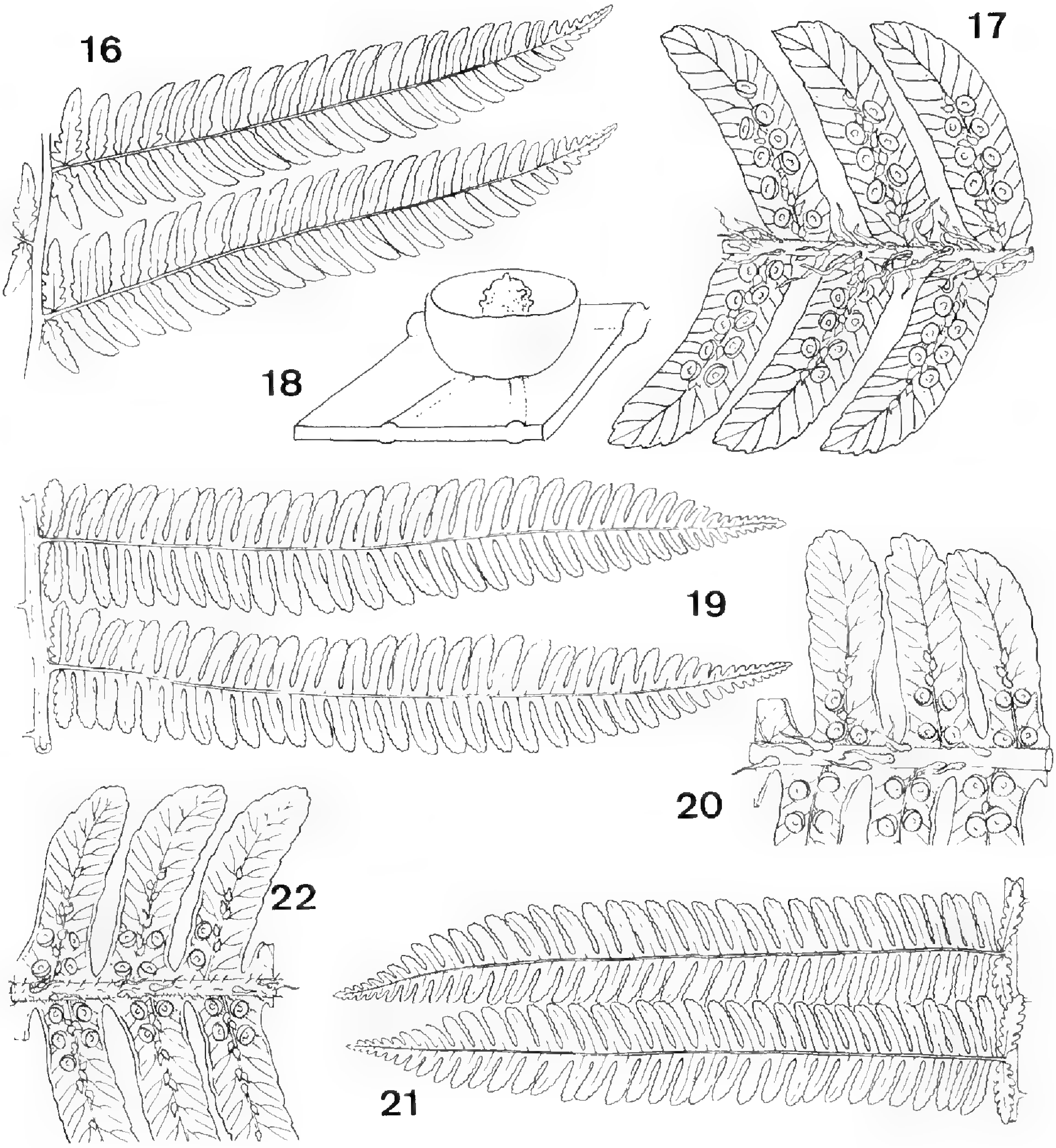
24. Lamina tripinnate (rarely quadripinnate); veins glabrous to sparsely squamulose; indusia sphaeropteroid, glabrous; width/length quotient of middle pinnae ca. 0.34. [Costa Rica, Panama]. .... 30. *A. polystichoides.*

23. Indusia hemitelioid; basal pinnae often subaphlebioid. [SE Brazil, Argentina]. .... 22. *A. setosa.*

1. **Alsophila nockii** (Jenman) Tryon, Contr. Gray Herb. **200:** 29. 1970. FIGURES 16–18.

Cyathea nockii Jenman, J. Bot. **17:** 257. 1879. TYPE: Jamaica, Parish St. Andrew, Cinchona, *Nock 107* (holotype, presumably at K, not seen). POSSIBLE ISOTYPE: Jamaica, *Nock s.n.,* s.d. (US!).

Stem prostrate, to 20 cm long and 2 cm in diameter. Leaves 0.3–1.2 m by 11–26 cm; petiole 1–3 cm long, brown, base with persistent, tan to brown, often light-margined, lance-ovate to lanceolate scales with 1 apical seta; lamina pinnate-pinnatisect to bipinnate, the base gradually tapering, the apex gradually tapering, acuminate, the rachis stramineous, invested with lanceolate, flexuous, whitish to bicolorous scales with 1 apical seta (occasionally few marginal setae) and many rusty-brown trichomes beneath; pinnae 5.5–13.5 by 1–2.4 cm, sessile, conspicuously broader at base, gradually tapering at apex, adjacent ones widely spaced, the pinna-rachis with few stiff, brown trichomes beneath, base with lanceolate, flexuous, whitish to bicolorous scales with 1 apical seta (rarely with few marginal setae), these grading into whitish, setate, bullate scales apically; pinnules 6–15 by 2.5–3.5 mm, margin becoming slightly serrate at apex, the

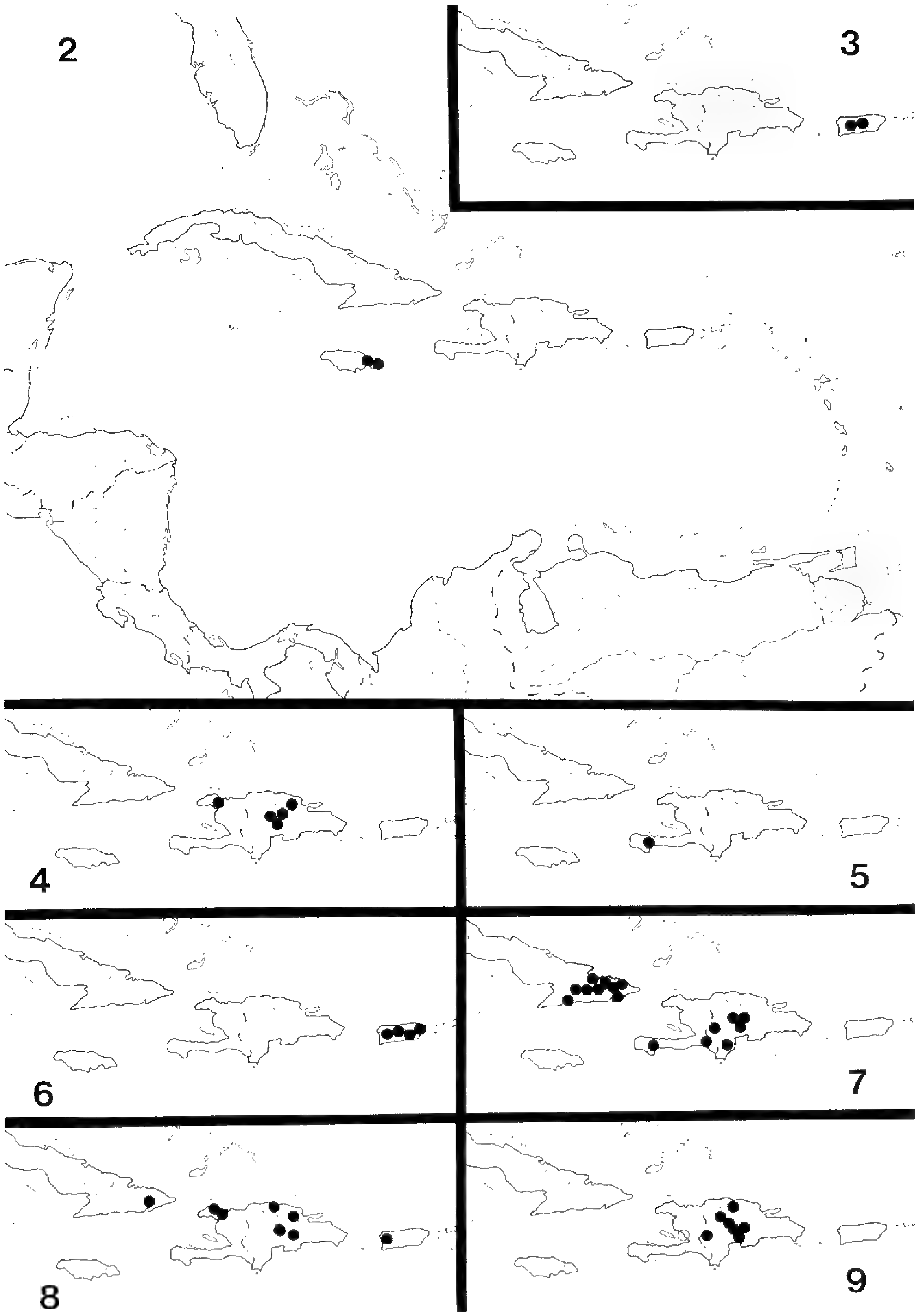


FIGURES 16–22. 16–18, *Alsophila nockii.* 16, 17, *Nock s.n.* (US *1,421,983*): 16, central pinnae, × .5; 17, central pinnules of central pinnae, × 2. 18, *Hart 13,* indusium, × 15. 19, 20, *A. amintae* (*Conant 1852*): 19, central pinnae, × .5; 20, central pinnules of central pinnae, × 2. 21, 22, *A. abbottii:* 21, *Conant 2118,* central pinnae, × .5; 22, *Conant 2121,* central pinnules of central pinnae, × 2.

basal ones much larger and more dissected, free to partially overlapping rachis, the pinnule-rachis with indument on undersurface similar to that of pinna-rachis, the veins 6 to 9 pairs, with tiny, antrorse, golden trichomidia beneath; indusia cyatheoid, glabrous.

DISTRIBUTION AND ECOLOGY. Jamaica, Blue Mountains (MAP 2). Steep, forested slopes; 910–1830 m alt.

REPRESENTATIVE SPECIMENS. **Jamaica.** No further locality: *Hart 13* (US), *Hart 2838* (MO), *Jenman s.n.,* September, 1879 (K), *Jenman s.n.,* 1874–79 (NY), *J. P. 42* (US). Blue Mountains: *Moore s.n.,* 1896 (GH). ST. THOMAS: Vinegar Hill, near Bath, *Maxon 2791* (US), *Underwood 1355* (NY). ST. ANDREW: Cinchona, *Harris 7322* (NY).



Maps 2–9. Distribution of species of *Alsophila* in the Greater Antilles: 2, *A. nockii*; 3, *A. amintae*; 4, *A. abbottii*; 5, *A. hotteana*; 6, *A. bryophila*; 7, *A. minor*; 8, *A. brooksii*; 9, *A. urbanii*.

Alsophila nockii is the smallest and rarest species of *Alsophila* in the Greater Antilles. Jenman (1898, p. 49) reported it as "common on a limited area of the disintegrated acclivous forest near Vinegar Hill," but it has rarely been collected since then.

2. **Alsophila amintae** Conant, Rhodora **83:** 149. 1981. FIGURES 19, 20.

Cyathea dryopteroides Maxon, Amer. Fern J. **14:** 99. 1925. TYPE: Puerto Rico, near Adjuntas, Monte Cerrote, *Britton & Brown 5424* (holotype, US!; isotypes, GH!, MO!). *Alsophila dryopteroides* (Maxon) Tryon, Contr. Gray Herb. **200:** 29. 1970, not *Alsophila dryopteroidea* Brause (= *Thelypteris dryopteroidea* (Brause) Reed), or *Alsophila dryopteridoides* Domin (= *Trichipteris dichromatolepis* (Fée) Tryon).

Stem erect, to 1.3 m tall and 5.1 cm in diameter. Leaves 0.5–1.6 m by 16–43 cm; petiole 1.3–3.5 cm long, purplish brown, the base with deciduous, golden-brown, concolorous to occasionally lighter-margined, lanceolate scales with 1 apical seta; lamina pinnate-pinnatifid, the base gradually tapering, the apex gradually tapering and acuminate, the rachis purplish brown, deciduously puberulous beneath; pinnae 8–20 by 1.3–3 cm, sessile or nearly so, broadest at base, gradually tapering at apex, adjacent ones widely spaced, lowermost reduced and subaphlebioid, the pinna-rachis with scales on undersurface bicolorous, lanceolate, with 1 apical seta; pinnules 10–17 by 2.5–5 mm, margin becoming crenate to serrate at apex, the basal ones slightly larger and more dissected, partially overlapping rachis, the pinnule-rachis with scales on undersurface of base few, tan, bullate, with or without apical setae, the veins 7 to 9 pairs, with tiny, antrorse, golden trichomidia beneath; indusia cyatheoid, glabrous.

DISTRIBUTION AND ECOLOGY. Puerto Rico, Cordillera Central (MAP 3). Shaded ravines and cloud forest; 1000–1200 m alt.

REPRESENTATIVE SPECIMENS. **Puerto Rico.** Cordillera Central: Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 595* (GH, NY, US), *682* (GH, Herb. EVFS, Herb. JBRMM, IJ, K, NY), *683* (F, GH, NY, SV), *689* (GH, Herb. JBRMM), *Conant & Kitfield 2256* (SV), *2301* (GH), *2309* (US), *Sargent 3141* (US); Monte Guilarte, W of Adjuntas, ca. 85 km WSW of San Juan, *Conant 1700* (US), *1852* (K), *1853* (F), *1856* (NY), *1858* (GH).

The name *Alsophila amintae* appears here in its corrected form (with the epithet in the genitive); the error was kindly pointed out by K. U. Kramer (pers. comm.).

The basipetal transition from normal to subaphlebioid pinnae in *Alsophila amintae* is similar to that found in the *A. decrescens* group of Madagascar.

This species hybridizes with *Alsophila bryophila* and *A. portoricensis* on Monte Jayuya and Monte Guilarte, Puerto Rico.

3. **Alsophila abbottii** (Maxon) Tryon, Contr. Gray Herb. **200:** 29. 1970. FIGURES 21, 22.

Cyathea abbottii Maxon, Proc. Biol. Soc. Wash. **37:** 98. 1924. TYPE: Dominican Republic, Prov. Duarte [Pacificador], near San Francisco de Macorís, Loma Quita Espuela, *Abbott 2051* (holotype, US (3 sheets)!; isotypes, GH!, NY!).

Stem erect, to 1.6 m tall and 5.1 cm in diameter. Leaves 1.1–1.5 m by 30–42 cm; petiole 1.5–3.8 cm long, brown, base with deciduous, golden-brown, concolorous to occasionally lighter-margined, lanceolate scales with 1 apical seta; lamina pinnate-pinnatifid, the base gradually tapering, the apex gradually tapering, acuminate, the rachis brown, deciduously puberulous beneath; pinnae

14–21 by 2.1–3.2 cm, sessile, broadest at base, gradually tapering at apex, the adjacent ones contiguous, the lowermost ones reduced and subaphlebioid; the undersurface of pinna-rachis having stiff, erect trichomes, bicolorous, lanceolate scales with 1 apical seta, and tiny, brown squamules with or without apical setae; pinnules 10–17 by 3–4.5 mm, margin becoming serrate at apex, the basal ones much larger and more dissected, overlapping rachis, the pinnule-rachis with scales on undersurface of base rusty brown, bullate, with 1 apical seta, the veins 9 to 11 pairs, with tiny, antrorse, golden trichomidia beneath; indusia cyatheoid, glabrous.

DISTRIBUTION AND ECOLOGY. Hispaniola (MAP 4). Shaded montane rainforest; 725–1200 m alt.

REPRESENTATIVE SPECIMENS. **Haiti.** DÉP. DU NORD-OUEST: Haut-Piton, near Port de Paix, *Ekman H3728* (US). **Dominican Republic.** LA VEGA: Loma de la Campana, *Ekman H11515* (NY, US); between Bonao and El Río, *Jiménez & Marcano 3062* (US); Palo Aboqueteado, SW of Bonao, *Liogier 14806* (Herb. JBRMM); Firma de Banilejo, near Piedra Blanca, *Liogier & Liogier 19943* (Herb. JBRMM); Loma de la Sal, 25 km NE of Constanza, *Judd 1386–1389* (GH). DUARTE: Loma Quita Espuela, NE of San Francisco de Macorís, *Abbott 2145* (US), *Conant 2115* (GH), *2117* (US), *2118* (NY), *Ekman H1227* (US).

Alsophila abbottii is most closely related to *A. amintae,* of Puerto Rico. These species are similar in size and appearance, and on the undersurface of the pinna-rachis both have bicolorous, lanceolate scales with one apical seta. A relationship also exists between these species and *A. nockii* and *A. tussacii,* of Jamaica, which are the only other species of *Alsophila* in the Greater Antilles with this type of laminar scale.

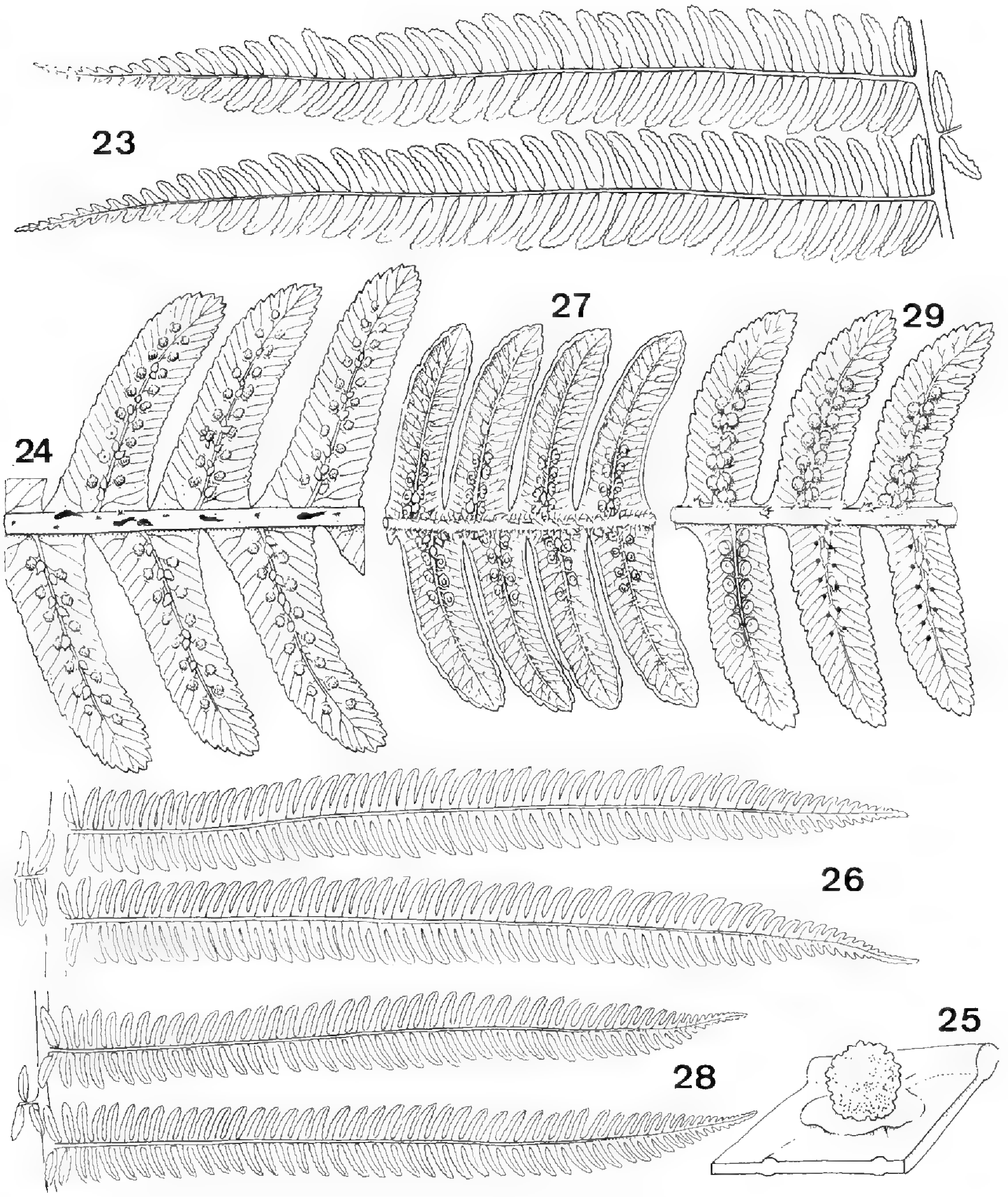
There is a gradual basipetal transition from normal to subaphlebioid pinnae in *Alsophila abbottii*—a trend similar to that found in the *A. decrescens* group of Madagascar.

Several collections from the Dominican Republic, Prov. La Vega, Loma de la Sal (e.g., *Judd 1388*) are unusual in that the pinnae are widely spaced. *Howard & Howard 8545* (A) is unusually pubescent and may represent a hybrid of *Alsophila abbottii* with *A. minor. Jiménez & Marcano 3062* has leaves that are more dissected than usual and may be a hybrid involving a species of *Alsophila* with more complex leaves.

4. **Alsophila hotteana** (C. Chr. & Ekman) Tryon, Contr. Gray Herb. **200:** 29. 1970. FIGURES 23–25.

Cyathea hotteana C. Chr. & Ekman, Kongl. Svenska Vetenskapsakad. Handl. III. **16**(2): 12. 1937. TYPE: Haiti, Dép. du Sud, near Camp Perrin, SE of Jérémie, Morne l'Étang, *Ekman H10383* (holotype, presumably in Herb. Ekman, Port-au-Prince, not seen; isotype, US!).

Stem erect, to ca. 2 m tall and 8 cm in diameter. Leaves ca. 2 m by 50 cm; petiole 1–4 cm long, brown, the base with deciduous, brown, lanceolate scales with 1 apical seta; lamina pinnate-pinnatifid to pinnate-pinnatisect, the base gradually tapering, the apex gradually tapering and acuminate, the rachis tan, deciduously puberulous beneath; pinnae to 24 by 3.5 cm, sessile, slightly broad-



FIGURES 23–29. 23–25, *Alsophila hotteana* (*Barrington 544*): 23, central pinnae, × .5; 24, central pinnules from central pinna, × 2; 25, indusium, × 15. 26, 27, *A. bryophila* (*Conant 1727*): 26, central pinnae, × .5; 27, central pinnules from central pinna, × 2. 28, 29, *A. minor* (*Gastony, G. C. Jones, & Norris 635*): 28, central pinnae, × .5; 29, central pinnules from central pinna, × 2.5.

er at base, gradually tapering at apex, the undersurface of pinna-rachis having few trichomes apically, acaroid scales, and dark-bodied, ovate scales with 1 to few apical setae; pinnules to 17 by 4.5 mm, margin becoming serrate at apex, the basal ones only slightly larger and slightly more serrate, not overlapping rachis, the undersurface of pinnule-rachis with acaroid scales and setate, bullate scales toward base and with few stiff trichomes apically, the veins 11 to 13 pairs, glabrous or with few tiny, antrorse, golden trichomidia beneath; indusia shallowly meniscoid to meniscoid, occasionally with 1 or 2 clefts, glabrous.

DISTRIBUTION AND ECOLOGY. Haiti, Massif de la Hotte (MAP 5). Cloud forest. The label on *Ekman H5423* ascribes this species to an area at 700 m; however, it is doubtful that suitable habitat exists below 1000–1200 m today due to extensive clearing of forest for agriculture.

REPRESENTATIVE SPECIMENS. **Haiti.** DÉP. DU SUD: Rivière Glace, *Holdridge 2175* (NY); Pic de Macaya, Massif de la Hotte, ca. 180 km WSW of Port-au-Prince, *Barrington 544* (GH); Jardins Coutard, near Camp Perrin, *Ekman H5243* (US).

Alsophila hotteana hybridizes with *A. woodwardioides,* producing an intermediate plant known as *A. confinis* (C. Chr.) Tryon (*Cyathea confinis* C. Chr.).

5. **Alsophila bryophila** Tryon, Rhodora **74:** 443. 1972. TYPE: Puerto Rico, Luquillo National Forest, near West Peak, *Gastony 12* (holotype, GH (4 sheets)!). FIGURES 26, 27.

Stem erect, to 7.3 m tall and 10 cm in diameter. Leaves 1.4–2.6 m by 41–58 cm; petiole 3.2–15 cm long, purplish brown, the base with deciduous, tan to brown, concolorous to bicolorous, lanceolate scales with 1 apical seta, occasionally with 1 pair of disjunct pinnae and gap of 6–15.2 cm between these and second pair; lamina pinnate-pinnatifid, the base gradually tapering to abruptly narrowed in plants with gap between basal and second pairs of pinnae, the apex gradually tapering and acuminate, the rachis purplish brown, densely invested with tan trichomes throughout; pinnae 15–31 by 1.6–3.8 cm, sessile, slightly broader at base, gradually tapering at apex, the undersurface of pinna-rachis densely pubescent, occasionally with few bullate scales at base; pinnules 7–13 by 2–3.5 mm, margin entire to serrulate at apex, the basal ones slightly larger, partially overlapping rachis, the pinnule-rachis pubescent above and beneath, base of undersurface with whitish, nonsetate, bullate scales, the veins 11 to 15 pairs, pubescent above and beneath and with abundant tiny, antrorse, golden trichomidia beneath; indusia meniscoid, glabrous.

DISTRIBUTION AND ECOLOGY. Puerto Rico; Sierra de Luquillo, Sierra de Cayey, Cordillera Central (MAP 6). An understory species in upper montane and elfin forest; 750–1200 m alt. (occasionally below 750 m in protected river valleys).

REPRESENTATIVE SPECIMENS. **Puerto Rico.** Sierra de Luquillo: no further locality, *Wilson 170* (NY); Pico del Este, *Conant & Kitfield 2325* (GH); Pico del Oeste, *Howard 15722, 15725, 16376* (A), *Howard et al. 15645* (A), *Howard & Nevling 15740, 16004, 16014* (A), *Schafer 3305* (GH, MO), *3632* (F, NY), *Sintenis 1480* (GH); Mount Britton, *G. N. Jones 10996, 11009* (GH); El Yunque, *Blomquist 11942* (F), *Conant 1565* (GH), *1647* (K), *Conant & Kitfield 2335* (GH, NY, US), *Cowles 408* (US), *Hess & Stevens 2951* (NY), *Little 21606* (GH), *Scamman 6519* (GH), *W. H. Wagner s.n.,* 14 May 1944 (GH); La Mina, *Conant 1599* (SV), *1600, 1602* (HB); El Cacique, *Conant 1587* (GH), *1588* (US), *1589* (NY), *1591* (F); El Toro Trail, *Conant 1754* (GH), *Conant & Kitfield 2338* (K); El Toro, *Conant 1726, 1727* (GH). Sierra de Cayey: Cerro la Santa, *Conant 1625* (GH). Cordillera Central: Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 688* (GH), *1811* (US), *2003* (F, Herb. EVFS, SV), *Conant & Kitfield 2253* (GH), *2255* (US), *2268* (F), *2270* (K), *2320* (NY); Monte Guilarte, ca. 85 km WSW of San Juan, *Conant 1918* (F, K, NY, US), *1921* (GH, NY, US).

Alsophila bryophila was formerly known as *Cyathea pubescens*. The latter is *A. auneae* and is endemic to Jamaica.

This species is subject to damage by a lepidopteran larva that chews on the sori, making tunnels of a mixture of spores, sporangia, and silk on the undersurface of the leaf and undoubtedly reducing spore output.

Leaves of specimens of *Alsophila bryophila* from the Cordillera Central are more tapered at the base, have shorter petioles, and have more closely spaced pinnae than those of specimens from the Sierra de Luquillo. The few existing specimens from the Sierra de Cayey are similar to plants from the Sierra de Luquillo.

The gap occasionally found between the basal pinnae and the main portion of the lamina in *Alsophila bryophila* isolates the basal pinna-pair, a condition characteristic of the *A. dregei* group in Madagascar. *Alsophila bryophila* has the pinnate-pinnatifid leaf architecture of the *A. decrescens* group of Madagascar.

Alsophila bryophila hybridizes with *A. amintae* in the Cordillera Central, and with *A. portoricensis* in the Cordillera Central and the Sierra de Luquillo. Hybrids between *A. bryophila* and *A. portoricensis* are to be expected in the Sierra de Cayey, where the two species commonly occur together.

6. **Alsophila minor** (D. C. Eaton) Tryon, Contr. Gray Herb. **200:** 29. 1970. FIGURES 28, 29.

Cyathea minor D. C. Eaton, Mem. Amer. Acad. Arts, n.s. **8:** 215. 1860. TYPE: Cuba, Prov. Oriente, near Guantánamo, Monte Verde, *Wright 949* (holotype, YU!; isotypes, GH!, MO (2 sheets)!, US!).

Cyathea tenuis Brause *in* Urban, Symb. Antill. **7:** 155. 1911. TYPE: Cuba, Prov. Oriente, Pinal de Santa Ana, *Eggers 5171B* (holotype, not seen; isotypes, K! (photos GH!, US!), NY!).

Stem erect, to ca. 7 m tall and 11 cm in diameter. Leaves 1.7–2.5 m by 20–53 cm; petiole 1.5–13 cm long, dark- to purplish-brown, the base having deciduous, uniformly brown, lanceolate scales with 1 apical seta, occasionally having 1 to 3 pairs of disjunct, subaphlebioid pinnae and gap of 11–42 cm between these and first pair of regular pinnae; lamina pinnate-pinnatifid to pinnate-pinnatisect, the base gradually tapering to abruptly narrowed in plants with gap between basal subaphlebioid pinnae and first pair of regular pinnae, the apex gradually tapering and acuminate, the rachis brown to stramineous, deciduously puberulous to persistently pubescent, occasionally with few acaroid scales beneath; pinnae 10–27 by 1.5–3.6 cm, sessile, slightly narrower to slightly broader at base, gradually tapering at apex, the undersurface of pinna-rachis sparsely to densely pubescent and invested with subbullate, setate scales that occasionally grade into acaroid scales, with bicolorous, lanceolate scales having a single apical seta, and often with marginal setae; pinnules 8–20 by 2–5 mm, margin becoming serrate at apex, the basal ones shorter to slightly larger and more dissected, overlapping rachis, the undersurface of pinnule-rachis pubescent and with whitish, setate, bullate scales, the veins 10 to 14 (rarely 16) pairs, pubescent and sometimes with tiny, antrorse, golden trichomidia beneath, glabrous (rarely with few scattered trichomes) above; indusia cyatheoid, pubescent.

DISTRIBUTION AND ECOLOGY. Hispaniola and Cuba (MAP 7). Wet montane forest; 450–2500 m alt.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: *Eggers 5252* (F), *Wright 893* (GH); Cerro de la Mina, 100 km N of Santiago, *Clément 6732* (US); Sierra de Buena Vista, ca. 80 km WNW of Santiago, *Ekman 3873* (NY, US), *Shafer 4454* (NY); Sierra Maestra, Pico Turquino, ca. 100 km W of Santiago, *Acuña 6731* (NY), *Ekman 14545* (NY), *León & Ekman 11151* (NY); La Bayamesa, near Pico Turquino, *Morton 9346, 9362* (US); Sierra de Nipe, Mayarí, ca. 80 km N of Santiago, *Ekman 4041* (US), *Morton & Acuña 3193* (GH, US); Sierra del Cristal, ca. 80 km NE of Santiago, *Clément 3976* (US), *Ekman 6854* (US); Sierra de Moa, ca. 130 km NE of Santiago, *Acuña 12351* (US), *Alain 3278* (US), *Shafer 8033, 8224* (NY); Cuchillas de Toa, Finca la Prenda, ca. 10 km N of Guantánamo, *Hioram 4107,* on Dec. 29 in part (GH), on Dec. 30 in part (US), *5009* (US), *Maxon 4134* (GH, NY, US), *Shafer 4154* (NY, US). **Haiti.** DÉP. DU SUD: Torbec, Massif de la Hotte, ca. 180 km WSW of Port-au-Prince, *Ekman H5334* (S). DÉP. DE L'OUEST: Morne la Visite, Massif de la Selle, SE of Port-au-Prince, *Ekman H1440* (S). **Dominican Republic.** SAN RAFAEL–INDEPENDENCIA: Sierra de Neiba, along Carretera Internacional, *Gastony, G. C. Jones, & Norris 426, 629, 630* (GH), *631* (GH, NY), *632* (GH), *633* (GH, NY), *634* (GH), *635* (GH, NY), *636* (GH). BARAHONA: Mingo, *Fuertes 1547* (F, NY, US); Montiada Nueva, *Howard & Howard 8563* (GH), *Judd, Liogier, & Liogier 1087* (GH). AZUA: between Valle Nuevo and Azua, *G. C. Jones & Norris 1129* (NY). PERAVIA: Loma Lucia, near San José de Ocoa, *Ekman H12009* (S). LA VEGA: between Valle Nuevo and La Horma, *Conant 2047* (K), *2049* (GH, NY, US), *Gastony, G. C. Jones, & Norris 728, 736* (GH, NY), *Judd 1223* (GH); between Constanza and Valle Nuevo, *Conant 2024* (GH, K), *Türckheim 3115* (GH, MO, NY); Ciénaga, N of Constanza, *Liogier 17067* (Herb. JBRMM); Los Tablones, NW of Constanza, *Gastony, G. C. Jones, & Norris 321* (GH, NY); Loma de la Sal, 25 km NE of Constanza, *Judd 1390* (GH).

Alsophila minor is most closely related to *A. bryophila,* of Puerto Rico. These are the only species of *Alsophila* in the Greater Antilles known to have the unusual "droop-tip" type of leaf vernation and occasionally to have a gap between the basal 1 to 3 pairs of pinnae (or subaphlebioid pinnae) and the next higher pinna-pair. These species may also be related to *A. hotteana,* which has scales like those of *A. minor* and an indusium resembling that of *A. bryophila,* and which is similar in size and appearance to both species.

Cuban material of *Alsophila minor* generally has smaller, less aphlebioid basal pinnae and a somewhat more slender stem than specimens from Hispaniola; however, a few Cuban specimens do show moderately well developed subaphlebioid basal pinnae, and a few from Hispaniola have basal pinnae that are hardly subaphlebioid.

The undersurface of the rachis of Cuban specimens is pubescent and is generally without acaroid scales. With the exception of *Morton 9346,* material with acaroid scales on the undersurface of the rachis is usually *Alsophila balanocarpa.* The Morton specimen is not *A. balanocarpa* by virtue of its nonspiny petiole, but it may represent a hybrid between this species and *A. minor. Acuña 6731* is unusual in having segments that are quite pubescent above—as in *A. bryophila.*

Some collections of this species are mixed. For example, *Eggers 5252* at US is *Alsophila woodwardioides*, while *Eggers 5252* (F) is *A. minor.*

There is usually a gradual basipetal transition from pinnae to subaphlebioid pinnae in *Alsophila minor*—a trend similar to that found in the *A. decrescens* group of Madagascar.

Alsophila minor hybridizes with *A. woodwardioides*, producing an intermediate plant known as *Cyathea irregularis* Brause. A specimen (*Howard & Howard 8545*) with pinna shape and leaf texture more like those of *A. abbottii* suggests that it may also hybridize with *A. abbottii* on Montiada Nueva, Prov. Barahona, Dominican Republic. An unusual series of collections by *Gastony, G. C. Jones, & Norris* (nos. *629* to *636*) from the Sierra de Neiba, between San Rafael and Independencia provinces, Dominican Republic (near the Haitian border), includes specimens with truly aphlebioid basal pinnae and with larger than usual middle pinnae. This suggests that the specimens might represent hybrids with *A. urbanii*, which was also growing in the vicinity.

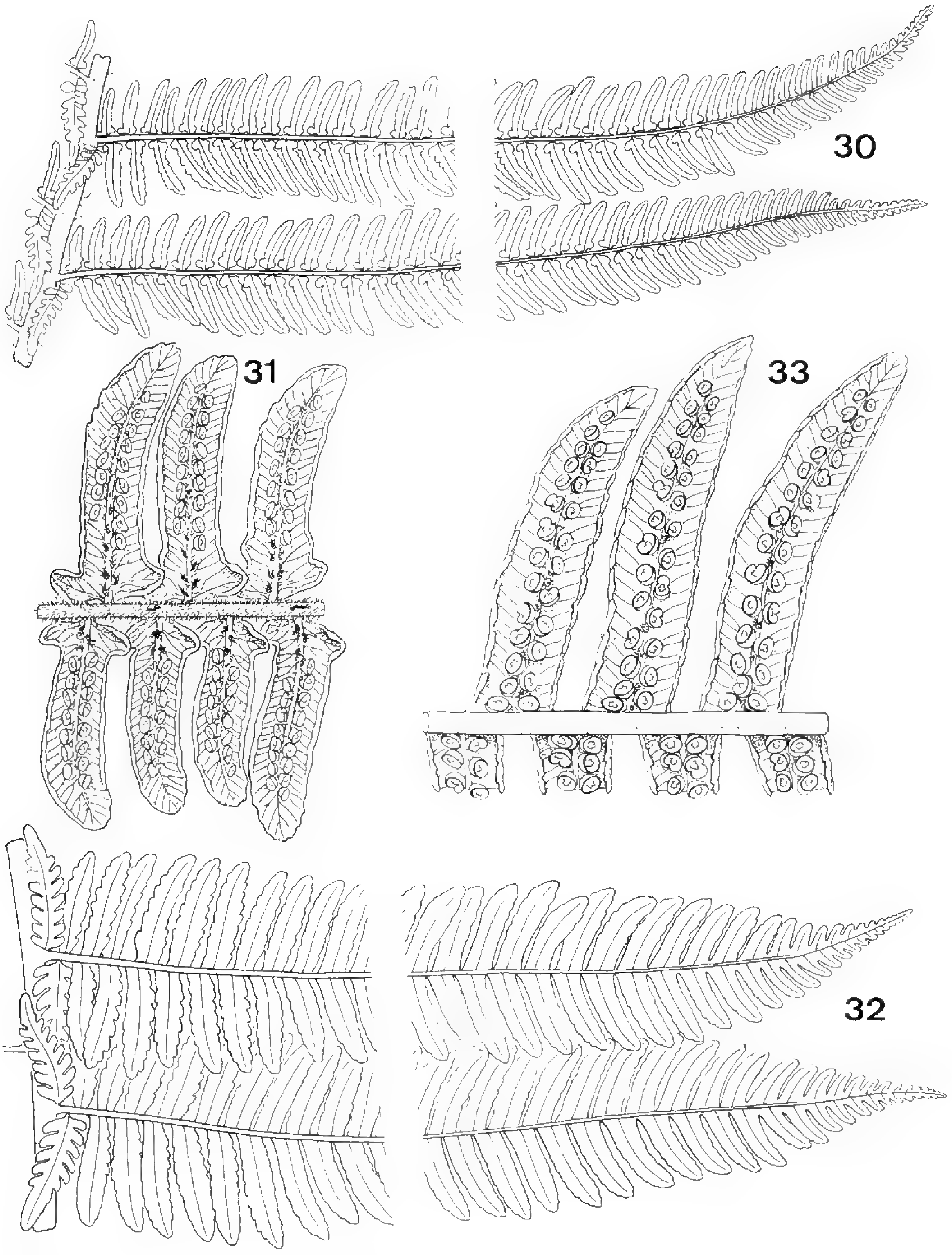
7. **Alsophila brooksii** (Maxon) Tryon, Contr. Gray Herb. **200:** 29. 1970.
FIGURES 30, 31.

Cyathea brooksii Maxon, Contr. U.S. Natl. Herb. **13:** 24. 1909. TYPE: Cuba, Prov. Oriente, Yateras, Finca las Gracias, *Maxon 4474* (holotype, US!; isotype, NY!).

Stem prostrate, to 43 cm long and 6.3 cm in diameter. Leaves 0.9–2.1 m by 24–62 cm; petiole 35–78 cm long, brown, the base having deciduous to persistent, heavily indurated, short- to long-deltoid scales with blackish body, lighter margin, and 1 apical seta; lamina pinnate-pinnatifid to bipinnate, the base abruptly narrowed, the apex gradually tapering and long-acuminate, occasionally nearly acute, the rachis brown to stramineous, pubescent beneath; pinnae 13–21 by 1.6–4 cm, sessile to short-stalked, slightly narrower to slightly broader at base, gradually tapering at apex, the undersurface of pinna-rachis pubescent and having acaroid scales and short to long, lanceolate scales with marginal and apical setae; pinnules 11–20 by 3–4 mm, margin entire to crenulate at apex, the basal ones slightly shorter to longer and more dissected, occasionally overlapping rachis, the undersurface of pinnule-rachis pubescent and with abundant acaroid scales, occasionally with dark, setate, lanceolate scales, the veins 12 to 18 pairs, undersurface with or without few trichomes, and with abundant tiny, antrorse, golden trichomidia; indusia cyatheoid, pubescent.

DISTRIBUTION AND ECOLOGY. Puerto Rico, Hispaniola, and Cuba (MAP 8). Shaded ravines along streams and forested slopes; 250–950 m alt. Usually on serpentine soils in Puerto Rico and Hispaniola, and to be expected in Cuba wherever such soils occur in wet mountains.

REPRESENTATIVE SPECIMENS. **Haiti.** DÉP. DU NORD-OUEST: Morne Baron, near St. Louis du Nord, *Ekman H3864* (US), *H3864a* (GH, NY), *H3864b* (F). DÉP. DU NORD: Morne Brigand, W of Port Margot, *Ekman H2874* (US). **Dominican Republic.** PUERTO PLATA: Pico Isabel de Torres, *Liogier, Liogier, & Melo 23490* (Herb. JBRMM). DUARTE: Loma Quita Espuela, NE of San Francisco de Macorís, *Abbott 2052, 2148* (GH, US), *2054* (US), *Conant 2141, 2142* (GH), *Ekman H12278* (US). LA VEGA: La Manaclita, 16 km S of La



FIGURES 30–33. 30, 31, *Alsophila brooksii:* 30, *Conant 2142,* central pinnae (22 cm long), × .5; 31, *Britton & Cowell 4223,* central pinnules of central pinna, × 2. 32, 33, *A. urbanii:* 32, *Conant 2017,* central pinnae, × .5; 33, *Gastony, G. C. Jones, & Norris 384,* central pinnules from central pinna, × 1.5.

Vega, *Liogier 11482* (Herb. JBRMM). SAN CRISTÓBAL: Río Isabel, near Altagracia, *Ekman H11195* (US). **Puerto Rico.** Vic. of Maricao: *Britton & Cowell 4223* (F, GH, MO, NY, US), *Conant 676, 677* (GH), *1656* (K), *1681* (US), *1923, 1924* (NY), *Hess 182, 349* (US), *7008* (NY), *Sargent 404, 636* (US).

Alsophila brooksii hybridizes with *A. portoricensis* in Puerto Rico and with *A. fulgens* in the Dominican Republic.

8. **Alsophila urbanii** (Brause) Tryon, Contr. Gray Herb. **200:** 29. 1970. FIGURES 32, 33.

Cyathea urbanii Brause *in* Urban, Symb. Antill. **7:** 151. 1911. TYPE: Dominican Republic, Prov. La Vega, near Constanza, *Türckheim 3076* (holotype, B, photo and fragment US!).

Cyathea urbanii var. *conferta* Brause *in* Urban, Symb. Antill. **7:** 152. 1911. TYPE: Dominican Republic, Prov. La Vega, near Constanza, *Türckheim 3076b* (holotype presumably at B, not seen; isotypes, GH!, US!).

Stem prostrate to decumbent, to 40 cm long and 6.5 cm in diameter. Leaves 1.4–3 m by 39–63 cm; petiole 14–58 cm long, stramineous, the base occasionally with aphlebiae and with deciduous, fleshy, brown, lanceolate scales, these grading into more typical dry, brown, lanceolate scales with 1 apical seta; lamina pinnate-pinnatifid to pinnate-pinnatisect, the base abruptly narrowed, the apex gradually tapering and acuminate, the rachis stramineous, deciduously invested with tiny, setate squamules; pinnae 19–33 by 4–8 cm, sessile or nearly so, broadest at base, gradually tapering at apex, undersurface of pinna-rachis with acaroid scurf, acaroid scales, and marginally setate, ovate scales; pinnules 21–40 by 5–8 mm, margin entire to crenate, the basal ones larger and more dissected, often overlapping rachis, the undersurface of pinnule-rachis with setate squamules and acaroid scales at base, and with golden squamules throughout, the veins 13 to 24 pairs, glabrous to sparsely pubescent and with abundant tiny, antrorse, golden trichomidia beneath; indusia subcyatheoid to deeply cyatheoid, occasionally with 1 or 2 clefts, sometimes slightly pubescent.

DISTRIBUTION AND ECOLOGY. Dominican Republic (MAP 9). In shaded ravines along streams at lower elevations and in cloud forest at higher altitudes; 800–2000 m alt.

REPRESENTATIVE SPECIMENS. **Dominican Republic.** AZUA: Sierra de Ocoa, N of Azua, *Ekman H11815* (US), *H11628* (S). LA VEGA: Loma Culo de Maco, SW of Constanza, *Ekman H6339* (S, US); Loma de la Sal, 25 km NE of Constanza, *Judd 1400* (A); Loma del Campanario, N of Constanza, *Conant 2014* (NY), *2015* (US), *2016* (GH), *2017* (K), *Liogier 16071* (Herb. JBRMM); Loma de la Vieja, near Constanza, *Ekman H14057* (S); La Ciénaga, N of Constanza, *Jiménez 3968, 4013* (US); Constanza, *Seifriz 5* (US); between Constanza and Valle Nuevo, *Conant 2075* (GH); between Valle Nuevo and La Horma, *Conant 2050* (GH); along road from Bonao to Constanza, *Lavastre 2016* (NY), *2041* (A); Palo Aboqueteado, SW of Bonao, *Liogier 14807* (Herb. JBRMM). SAN RAFAEL–INDEPENDENCIA: Sierra de Neiba, along Carretera Internacional, *Gastony, G. C. Jones, & Norris 577* (GH, NY). SANTIAGO: Pico Diego de Ocampo, N of Santiago, *Conant 2102* (GH), *2103* (US), *2104* (K), *Ekman H13211* (NY), *Jiménez 4551* (US), *Judd 1521, 1523, 1524* (GH). SANTIAGO–SAN JUAN: *Gastony, G. C. Jones, & Norris 384* (GH, NY).

The relationship of *Alsophila urbanii* to other species of *Alsophila* in the Greater Antilles is not clear. The prostrate stem and long petiole suggest a link with *A. brooksii,* while its aphlebiae may indicate a relation to *A. minor.* The closest relative of *A. urbanii* appears to be *A. zakamenensis,* of Madagascar, which has similarly large pinnules and well-developed aphlebiae.

There is nothing distinctive about Brause's var. *conferta.* With more material now available, it is clear that both original collections (*Türckheim 3076* and *3076b*) fit well within the normal variation of the species.

This species may hybridize with *Alsophila minor* in the Sierra de Neiba, between Prov. San Rafael and Prov. Independencia near the Haitian border.

9. **Alsophila rupestris** (Maxon) Gastony & Tryon, Amer. J. Bot. **63:** 743. 1976. FIGURES 34, 35.

Cyathea rupestris Maxon, J. Arnold Arbor. **27:** 438. 1946. TYPE: Colombia, Dept. Norte de Santander, region of Sarare, between Junín and Córdoba, Río Margua, *Cuatrecasas 13396* (holotype, US!; isotypes, F!, US!).

Stem presumably erect, length unknown, to 1.5 cm in diameter. Leaves 41–47 by 10–11.5 cm; petiole 4–6 cm long, black, the base with persistent, heavily indurated, deltoid scales with blackish body, lighter margin, and 1 apical seta; lamina pinnate-pinnatifid, the base abruptly narrowed, the apex gradually tapering and long-acute, the rachis black, glabrous toward base, pubescent with stiff, brown trichomes toward apex; pinnae 5–5.8 by 1.2–1.3 cm, sessile, slightly narrower to equal at base, tapering to rather blunt tip at apex, undersurface of pinna-rachis with stiff, brown trichomes; pinnules 6–7 by 3 mm, margin entire, the basal ones equal to or slightly smaller than middle ones, the inferior basal ones with auricle overlapping rachis, the indument on undersurface of pinnule-rachis similar to that of pinna-rachis, the veins 5 to 7 pairs, with tiny, antrorse, golden trichomidia beneath; indusia cyatheoid, glabrous.

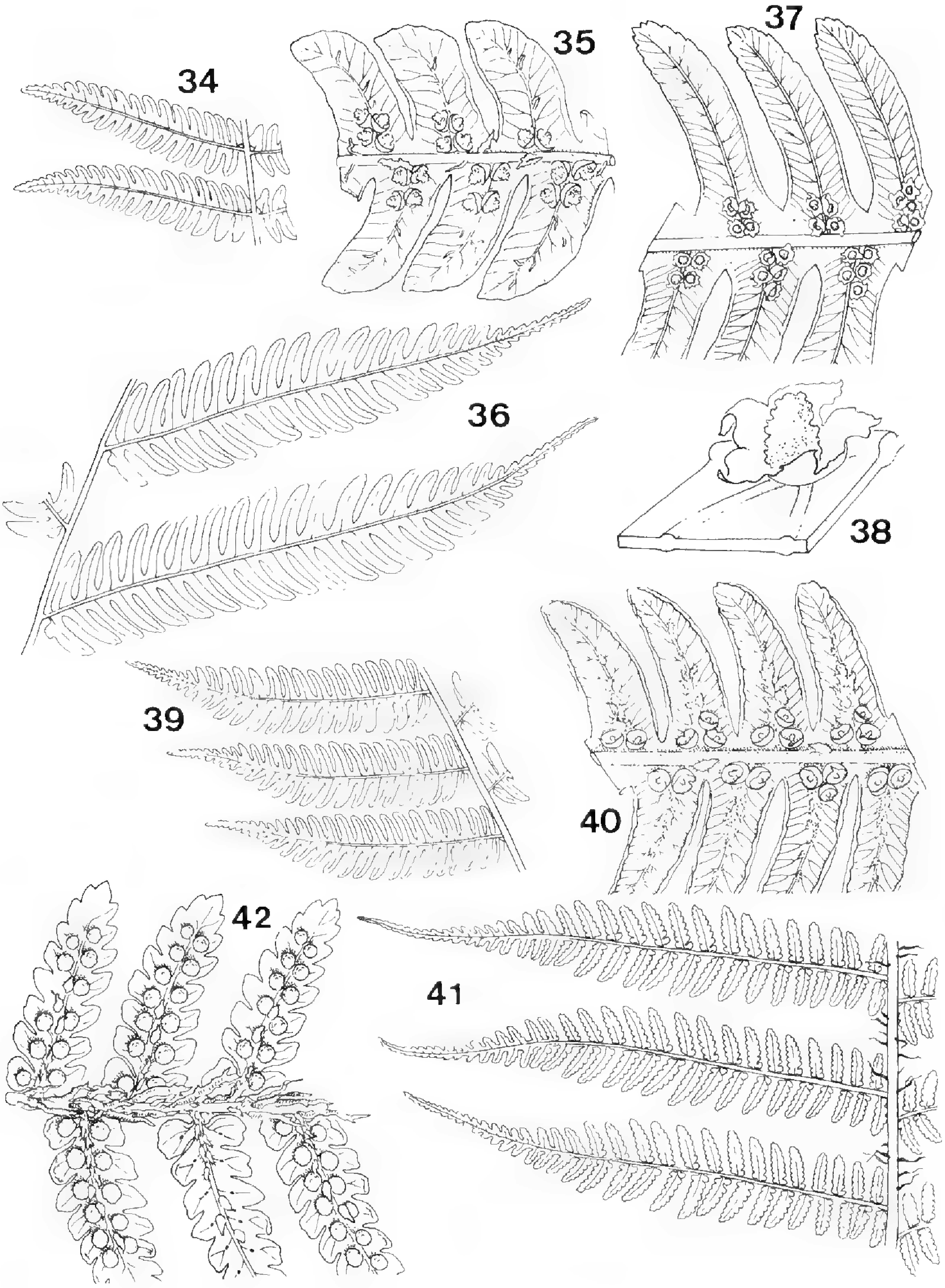
DISTRIBUTION AND ECOLOGY. Colombia, Dept. Norte de Santander, Río Margua, near Sarare (MAP 10). Known only from the type collection, 920–1240 m alt.

Alsophila rupestris is the smallest species of American *Alsophila.* Although it is similar in leaf architecture to species in the Greater Antilles, it does not have the laminar scales present in all of those species.

10. **Alsophila paucifolia** Baker *in* Hooker & Baker, Synopsis Fil. ed. 2. 546. 1874. TYPE: Ecuador, Montana de Canelos, *Spruce s.n.,* Oct. 1857 (holotype, K!, US (fragment)!). POSSIBLE ISOTYPES: Ecuador, *Spruce s.n.,* 1857–59 (K!); Ecuador, Canelos, *Spruce 5363* (P!). FIGURES 36–38.

Cyathea stübelii Hieron. Hedwigia **45:** 229. *t. 12, fig. 2.* 1906. TYPE: Ecuador, Prov. Tungurahua, between Baños and Jivaría de Píntuc, in valley of Río Pastaza, *Stübel 1007* (holotype, B!, photo GH!).

Stem erect, length unknown, to 1.8 cm in diameter. Leaves to ca. 1.5 m by ca. 40 cm; petiole 12–25 cm long, black, the base with persistent, heavily indurated, lanceolate scales with blackish body, lighter margin, and 1 apical seta; lamina pinnate-pinnatifid, the base abruptly narrowed, the apex gradually tapering and long-acuminate, the rachis black, glabrous; pinnae 15–18.5 by 2.9–4 cm, sessile, slightly narrower to equal at base, tapering to long-attenuate tip at apex, base of undersurface of pinna-rachis sparsely scurfy and with few deciduous, dark, indurated, deltoid scales with 1 apical seta; pinnules 18–22 mm by 4–4.5 mm, margin becoming serrulate at apex, the basal ones equal to or smaller than middle ones, not overlapping rachis, the undersurface of pin-



FIGURES 34–42. 34, 35, *Alsophila rupestris* (*Cuatrecasas 13396*): 34, central pinnae, × .5; 35, central pinnules from central pinna, × 2.5. 36–38, *A. paucifolia* (*Spruce 5363*): 36, central pinnae, × .5; 37, central pinnules from central pinna, × 2; 38, indusium, × 15. 39, 40, *A. engelii* (*White 1969240*): 39, central pinnules from central pinna, × .5; 40, central ultimate segments from central pinnule, × 2.5. 41, 42, *A. salvinii* (*Williams & Molina 10730*): 41, central pinnules from central pinna, × .5; 42, central tertiary segments from central pinnule, × 2.5.

nule-rachis sparsely scurfy, the veins 12 to 15 pairs, with tiny, antrorse, golden trichomidia beneath; indusia sphaeropteroid, variously ruptured in mature specimens, glabrous.

DISTRIBUTION AND ECOLOGY. Ecuador (MAP 11). Border of montane forest; ca. 1700 m alt.

REPRESENTATIVE SPECIMEN. **Ecuador.** PUTUMAYO: Río Mocoa between Sachamate and San Antonio, *Ewan 16695* (US).

Although the thin, sphaeropteroid indusia, rupturing at maturity, resemble those often found in *Alsophila engelii,* the closest relation of *A. paucifolia* seems to be *A. rupestris* of Colombia. Both of the latter species have unusually slender stems, black petioles and rachises, and dark, indurated scales at the apex of the stem and the base of the petiole.

11. **Alsophila engelii** Tryon, Contr. Gray Herb. **200:** 29. 1970.

FIGURES 39, 40.

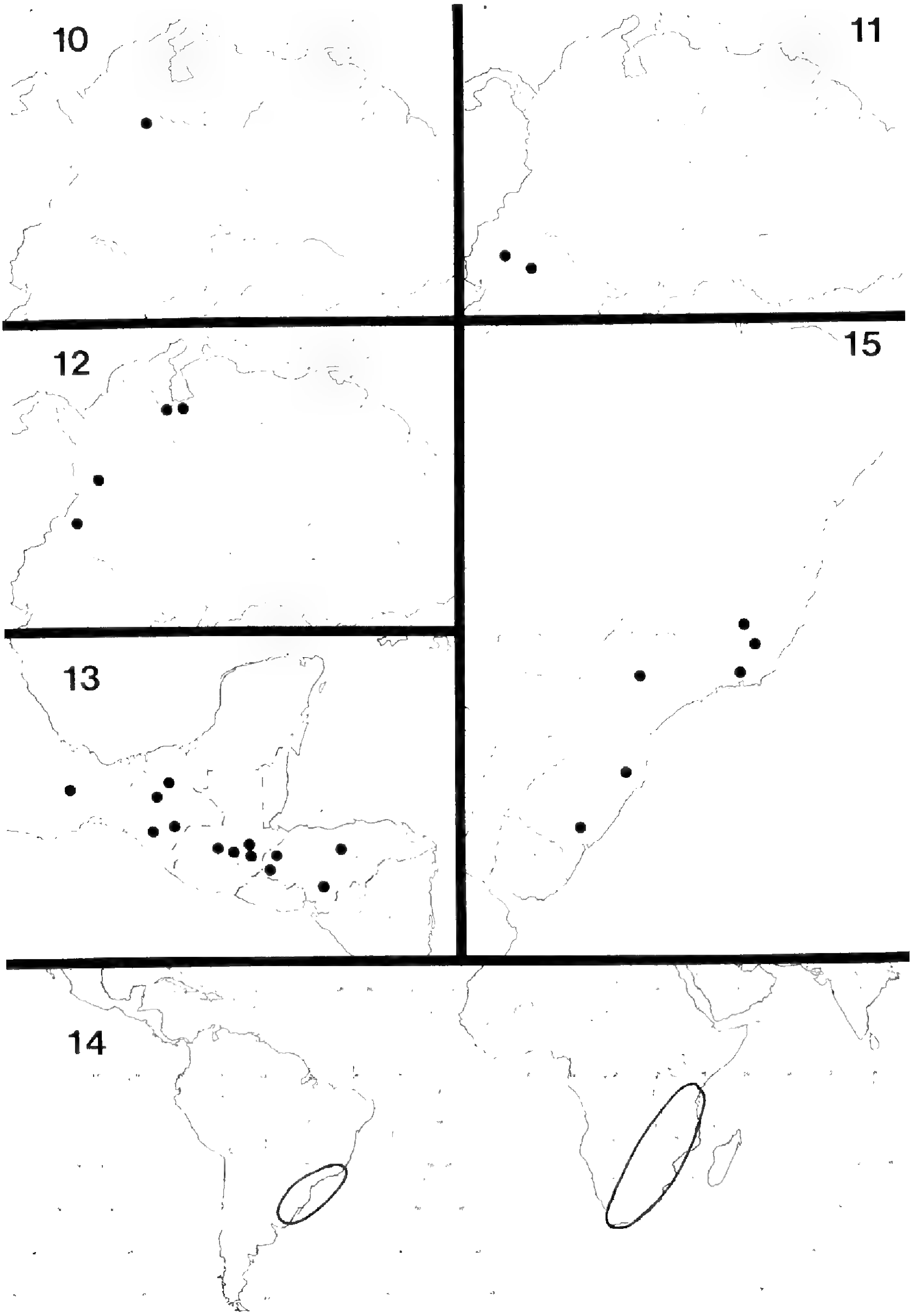
Cyathea elongata Karsten, Fl. Columb. **2:** 159 (sub *Cyathea erinacea*). *t. 183, figs. 15, II.* 1869. TYPE: Venezuela, Mérida, *Engel 138* (holotype, B!). Not *Alsophila elongata* Hooker, Sp. Fil. **1:** 43. 1844.

Stem erect, to ca. 11 m tall, diameter unknown. Leaves of unknown length and to 1.3 m broad; petiole 25 cm or more in length, smooth to tuberculate, brown, the base with deciduous, tan, lanceolate scales with 1 apical seta; lamina bipinnate-pinnatifid, the base narrowed, the apex gradually tapering and acuminate, the rachis tan to brown, undersurface deciduously invested with highly dissected, setate scales (appearing pubescent) and few tan to brown, lanceolate scales with 1 apical seta; pinnae 50–65 by 10–17.5 cm, sessile or nearly so, broadest at base, abruptly narrowing to long, slender tip at apex, undersurface of pinna-rachis with indument similar to that of rachis; pinnules 7–9.3 by 1–2 cm, pinnatifid, apex abruptly narrowed to long, slender tip, the basal ones equal to or slightly smaller than middle ones, not overlapping rachis, the undersurface of pinnule-rachis with flabellate to lanceolate, tan to brown, often partially indurated, multisetate scales and with highly dissected scales and/or trichomes; ultimate segments 6–10 by 2–3 mm, the margin becoming crenulate to serrulate at apex, the undersurface of midvein with scattered, translucent, brownish, setate, subbullate scales to densely invested with highly dissected scales, the veins 8 to 10 pairs, with whitish to tan trichomidia beneath; indusia deeply cyatheoid to sphaeropteroid, glabrous.

DISTRIBUTION AND ECOLOGY. Colombia and Venezuela (MAP 12). Mountains; 2000–2900 m alt.

REPRESENTATIVE SPECIMENS. **Colombia.** CAUCA: Cordillera Occidental, Cerro de Munchique, *Arbeláez & Cuatrecasas 6256* (US). CALDAS: Cordillera Central, Pinares, above Salento, *Pennell 9695* (GH, NY, US). **Venezuela.** MÉRIDA: *Bernardi 6198* (GH, NY); Carbonerra, near Mérida, *White 1969240* (GH), *White & Lucansky 1970143* (US).

The holotype of *Alsophila engelii* (*Engel 138*) is without a petiole; however, recent collections (e.g., *Pennell 9695* and *White 1969240*) similar to that spec-



MAPS 10–15. Distribution of species of *Alsophila* in Mexico and Central and South America: 10, *A. rupestris*; 11, *A. paucifolia*; 12, *A. engelii*; 13, *A. salvinii*; 14, *A. capensis* (Old and New World distribution); 15, *A. capensis* subsp. *polypodioides*.

imen in size, dissection, and indument of the lamina have nonspiny petioles and marginate petiole scales with a single apical seta.

There is considerable variation in the indument on the undersurface of the pinnule-rachis and the midveins of the ultimate segments. Some specimens (e.g., *Pennell 9695*) have multisetate, flabellate scales and dissected scales on the pinnule-rachis and a dense investiture of dissected scales on the midvein of the ultimate segments. Others, such as *White 1969240* and *Bernardi 6198,* are sparsely invested with flabellate scales and dissected scales.

Alsophila engelii was named for Franz Engel, collector and field artist, who contributed to the plates of Cyatheaceae in Karsten's *Flora Columbiae.*

12. **Alsophila salvinii** Hooker *in* Hooker & Baker, Synopsis Fil. 36. 1866. TYPE: Guatemala, Baja Verapaz, Chilasco, *Salvin & Goodman s.n.,* s.d. (holotype, K). POSSIBLE ISOTYPE: Guatemala, *Salvin s.n.,* s.d. (GH!). FIGURES 41, 42.

Alsophila munchii Christ, Bull. Herb. Boissier, II. 5: 743. 1905. TYPE: Mexico, Chiapas, San Pablo, *Münch 139* (fragment of holotype, NY!; isotype, US!).

Stem erect, to ca. 9 m tall, diameter unknown. Leaves to ca. 2.5 by 1.4 m; petiole to 0.5 m or more, slightly tuberculate, black, the base with up to 15 pairs of aphlebiae, densely invested with deciduous, appressed squamules and with persistent, brown, lanceolate scales having 1 apical seta; lamina tripinnate to rarely quadripinnate, the base abruptly narrowed, the apex gradually tapering and short-acuminate, the rachis black, slightly tuberculate, undersurface deciduously invested with appressed squamules; pinnae 40–77 by 15–34 cm, bipinnate to rarely tripinnate, stalked, slightly narrower at base, acuminate and tapering to long, slender tip at apex, undersurface of pinna-rachis with indument similar to that of rachis; pinnules 7.5–18 by 1.4–3.5 cm, pinnate to rarely bipinnate, apex gradually tapering to long, slender tip, the basal ones equal to or slightly smaller than middle ones, distant from rachis, the pinnule-rachis alate, undersurface with few to many dark brown, lanceolate scales having 1 to few apical setae, these grading into subbullate scales apically, and with acaroid scales; tertiary segments 7–20 by 2.5–5 mm, crenate to nearly pinnate at base, the base of undersurface of midvein with acaroid scales and with brown, setate, subbullate scales, these grading into bullate scales apically, the veins 8 to 12 pairs, glabrous; indusia lacking.

DISTRIBUTION AND ECOLOGY. Southern Mexico, Guatemala, and Honduras (MAP 13). Cloud forest; 910–2600 m alt.

REPRESENTATIVE SPECIMENS. **Mexico.** OAXACA: between Oaxaca and Tuxtepec, *Hellwig 408* (US), *Stone & Broome 2814* (GH, NY, US). CHIAPAS: Sierra de Soconusco, *Hernández & Sharp X336* (US); Cerro del Boquerón, *Purpus 6768* (US), *6769* (F, GH, NY, US); Yerba Buena Mission, *Tillet 636-4* (GH, US); between Canada Honda and Triumfo, *Xolocotzi & Sharp X336* (US). **Guatemala.** Without further locality, *Türckheim s.n.,* s.d. (NY). HUEHUETENANGO: between Xoxlac and Nucapuxlac, Sierra de los Cuchamotones, *Steyermark 48924* (F, US). EL QUICHÉ: *Aguilar 1220* (F). ALTA VERAPAZ: Chihot, *H. Johnson 959* (NY, US); near Tactic, *Stone & Stone 2706* (GH, NY); Cobán, *Türckheim 845* (GH, NY, US), *II 2027* (F, GH, MO, NY); Sierra de las Minas, *Steyermark 42538* (F, US). ZACAPA: between Loma el Picacho and Cerro de Monos, *Steyermark 42790* (F, GH, US). **Honduras.** Without further locality, *Williams & Molina 10730* (F, GH, MO, US). OCOTEPEQUE: Montecristo, Cordillera de Miramundo, *Molina, Burger, & Wallenta 16749* (NY); Cordillera Merendon, 20 km NW of Ocotepeque, *Molina 22104* (NY). FRANCISCO MORAZÁN: above San Juancito, *Williams, Molina, & Merrill 15637* (F, GH, US); La Tigra, S of San Juancito, *Molina 10253* (F, NY, US), *Molina et al. 16974* (NY); Monte San Juancito, near El Rosario, *Molina 23405* (NY); Monte Uyuca, *Molina 10674, 13619* (NY), *Morton 6932, 7173* (US), *Standley 4826* (F, US), *13550* (F, NY, US), *Standley & Williams 735* (F, GH), *738* (F).

Although *Alsophila salvinii* has black axes similar to those found in *A. paucifolia* and *A. rupestris,* it seems to be most closely related to the *A. boivinii* group of aphlebioid species in Madagascar and Borneo.

It appears that *Alsophila salvinii* has hybridized with *A. firma,* and that segregates of this cross have become stabilized via allohomoploidy, resulting in two distinct species: *A. tryoniana* and *A. polystichoides* (see Conant & Cooper-Driver, 1980).

13. **Alsophila capensis** (L. f.) J. Sm. London J. Bot. **1:** 666. 1842.

Stem erect, to ca. 4.5 m tall and ca. 15 cm in diameter. Leaves of unknown length by 64 cm; petiole to 40.5 cm long, smooth to slightly tuberculate, dark brown at base, becoming lighter above, the base with 1 to few pairs of highly dissected aphlebiae and with persistent to deciduous, brown, lanceolate scales having 1 apical seta; lamina bipinnate-pinnatifid, the base abruptly narrowed, the apex gradually tapering and short-acuminate, the rachis smooth to slightly tuberculate, with persistent to deciduous, brown, lanceolate scales having 1 apical seta, and occasionally with tan, appressed scurf; pinnae 24–53 by 9.5–19 cm, pinnate-pinnatifid, nearly sessile to conspicuously stalked, slightly narrower at base, acuminate to attenuate at apex, the undersurface of pinna-rachis with bullate scales, with tan to brown or dark brown, indurated, lanceolate scales having 1 apical seta, these sometimes tortuous and having light margin, and occasionally with appressed scurf; pinnules 5–11.5 by 1–2 cm, pinnatifid, sinuses between ultimate segments equilateral or inequilateral and directed toward base of pinnule, apex acuminate to attenuate, the basal ones equal to or slightly smaller than middle ones, not overlapping rachis, the undersurface of pinnule-rachis with bullate scales and with light brown or dark, indurated, lanceolate scales; ultimate segments 6–11 by 1.8–3 mm, the margin serrate, the undersurface of midvein with tan, bullate scales, sometimes also with small, dark, indurated, lanceolate scales, the veins 6 to 9 pairs, occasionally with tiny, antrorse, golden trichomidia beneath; indusia hemitelioid, glabrous.

DISTRIBUTION. Southeastern Africa and southeastern Brazil.

Alsophila capensis is the only species of Cyatheaceae to occur in both the Old and New World tropics (Holttum, 1981, as *Cyathea capensis*). Hooker (1844) and Tardieu-Blot (1941) have attributed this species to Java, but Holttum (1965) did not cite *A. capensis* as occurring there.

This species is differentiated into African and American subspecies that occupy similar latitudinal ranges in southeastern Africa and southeastern Brazil.

Key to Subspecies of *Alsophila capensis*

1. Undersurface of pinna-rachis with tan to brown, nonindurated, lanceolate scales; sinuses between ultimate segments of pinnules inequilateral at base. .... 13a. subsp. *capensis.*
1. Undersurface of pinna-rachis with dark brown to blackish, indurated, lanceolate scales, these sometimes tortuous and with light margin; sinuses between ultimate segments of pinnules equilateral at base. .... 13b. subsp. *polypodioides.*

13a. **Alsophila capensis** subsp. **capensis** FIGURES 43–45.

Polypodium capense L. f. Suppl. Pl. 445. 1781. *Cyathea capensis* (L. f.) J. E. Sm. Mém. Acad. Turin **5:** 417. 1793. *Aspidium capense* (L. f.) Sw. Synopsis Fil. 61. 1806. *Hemitelia capensis* (L. f.) Sprengel, Syst. Veg. 4. 126. 1827, not R. Br. Prodr. 158. 1810. *Cormophyllum capense* (L. f.) Newman, Phytologist **5:** 238. 1854. *Polystichum capense* (L. f.) Newman, *ibid.* TYPE: Union of South Africa, Cape of Good Hope, *Sparrmann s.n.* (LINN, not seen).

Trichomanes incisum Thunb. Pl. Capens. 173. 1800. TYPE: Union of South Africa, Cape of Good Hope, *Thunberg s.n.* (probably U, not seen).

Cyathea riparia Willd. Sp. Pl. ed. 5. 493. 1810. *Hemitelia riparia* (Willd.) Desv. Mém. Soc. Linn. Paris **6:** 322. 1827. *Amphicosmia riparia* (Willd.) Gardner, London J. Bot. **5:** 438. 1842. TYPE: Union of South Africa, Cape of Good Hope, *Herb. Willd. 20172* (B, not seen).

Trichomanes cormophyllum Kaulf. Enum. Fil. 266. 1824. TYPE: Union of South Africa, Cape of Good Hope, *Chamisso s.n.* (probably at LE, not seen).

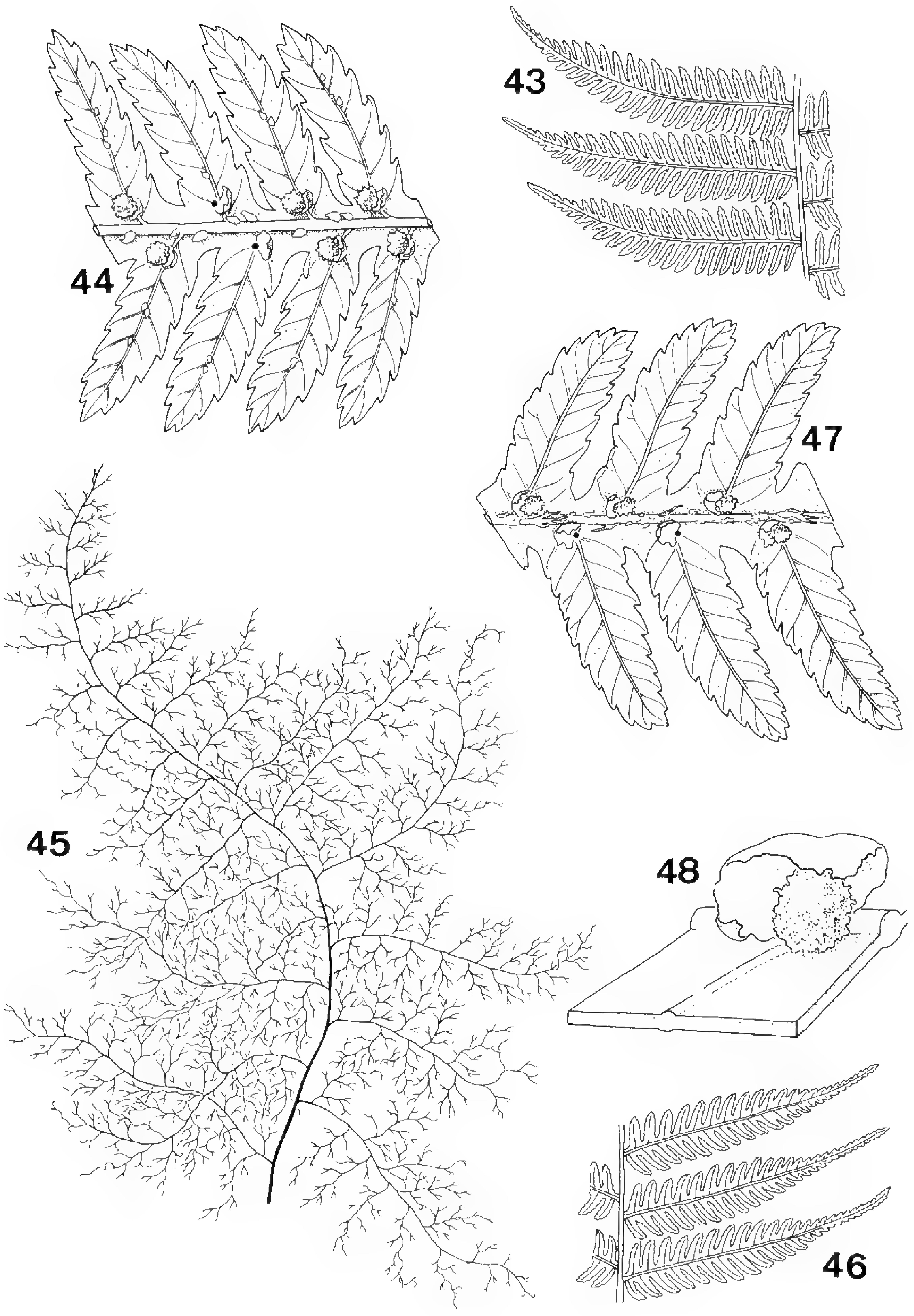
Stem erect. Petiole smooth to slightly tuberculate, with 1 to few pairs of highly dissected aphlebiae; lamina bipinnate-pinnatifid, base abruptly narrowed, apex gradually tapering and short-acuminate; pinnae pinnate-pinnatifid, slightly narrower at base, acuminate at apex, the undersurface of pinna-rachis with tan to brown, nonindurated, lanceolate scales with 1 apical seta; pinnules pinnatifid, sinuses between ultimate segments inequilateral and directed toward base of pinnules.

DISTRIBUTION AND ECOLOGY. Tanzania, Malawi, Zimbabwe, South Africa, and Swaziland (MAP 14). Shaded forests and along rivers, especially near waterfalls; 360–1820 m alt. Holttum (1981) reports *Alsophila capensis* (as *Cyathea capensis*) as occurring in Mozambique; however, he does not cite a specimen.

REPRESENTATIVE SPECIMENS. **Tanzania:** no further locality, *Peter 28018* (US). **Malawi:** Luchenya, *Brass 16600* (US). **Zimbabwe:** Inganga, *Chase 5671* (GH). **South Africa.** No further locality: *Burchell 5862* (GH), *Rogers 17502* (US), *Sim et al. 1573* (GH). NATAL: *Abraham 38* (GH, US), *Buchanan 519* (US), *Fisher & Schweickerdt 48* (US), *Rudatis 1551* (US), *Tidmarsh 2* (GH). CAPE OF GOOD HOPE: *Allen 3553* (US), *Cummings 315* (GH, US), *Dummer 1Dt* (GH), *Flanagan 1531* (US), *Kennedy 1853* (GH), *Rodin 1190* (US), *J. Smith 10* (GH), *Tryon & Tryon 6347, 6381* (GH). **Swaziland:** no further locality, *Schelpe 6181* (US).

Although I have not seen the type of *Polypodium capense,* it is undoubtedly *Alsophila capensis* since this is the only tree fern known to occur on the Cape of Good Hope (Adamson & Slater, 1950).

There is little known about the dimensions of leaves of *Alsophila capensis*; however, Sim (1891, p. 21) described a plant with fronds "six to nine feet long and two to three feet broad."



FIGURES 43–48. 43–45, *Alsophila capensis* subsp. *capensis*. 43, 44, *Tidmarsh 2:* 43, central pinnules from central pinna, × .5; 44, central ultimate segments from central pinnule, × 3. 45, *Fisher & Schweickerdt 48,* aphlebia, × .33. 46–48, *A. capensis* subsp. *polypodioides*. 46, *Gardner 5954,* central pinnules from central pinna, × .5. 47, 48, *Brade 16527:* 47, central ultimate segments from central pinnule, × 3; 48, indusium, × 15.

13b. **Alsophila capensis** subsp. **polypodioides** (Sw.) Conant, comb. et stat. nov. FIGURES 46–48.

Cyathea polypodioides Sw. Kongl. Vetensk. Acad. Handl. 78. 1817. TYPE: Brazil, Est. Minas Gerais, Villa Rica, *Freyreis s.n.* (holotype, S!).

Hemitelia gardneriana Presl, Gefässbündel Stipes der Farrn, 42. 1847 (preprint from Abh. Königl. Böhm. Ges. Wiss. V. **5:** 350. 1848). TYPE: Brazil, Est. Rio de Janeiro, Serra dos Órgãos, *Gardner 5954* (holotype, not located; isotypes, P!, US!, photo GH!).

Stem erect. Petiole smooth to slightly tuberculate, with 1 to few pairs of highly dissected aphlebiae; lamina bipinnate-pinnatifid, base abruptly narrowed, apex gradually tapering and acuminate; pinnae pinnate-pinnatifid, slightly narrower at base, acuminate to attenuate at apex, the undersurface of pinnarachis with dark brown to blackish, indurated, lanceolate scales, these sometimes tortuous and with light margin and 1 apical seta; pinnules pinnatifid, apex attenuate, sinuses between ultimate segments equilateral at base.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil (Minas Gerais, São Paulo, Rio de Janeiro, Paraná, Santa Catarina, Rio Grande do Sul; MAPS 14, 15). Along rivers in montane forest; 900–2000 m alt.

REPRESENTATIVE SPECIMENS. **Brazil.** No further locality: *Glaziou 3583* (NY); Taimbe, *Sehnem 6327* (US). MINAS GERAIS: Serra do Caparão, *Brade 17091* (NY); Villa Rica [Ouro Prêto], *Freyreis s.n.* (S); Carassa, *Vainio 33210* (GH). SÃO PAULO: Rio Castilho, *Jürgens 147* (S). RIO DE JANEIRO: Rio Roncador, Theresopolis, *Brade 9871* (NY); Serra dos Órgãos, *Brade 16527* (GH, MO, NY, US), *Glaziou 4440* (NY), *Luetzelburg 211a* (S), *18905* (NY). PARANÁ: Lucana, *Hialewstri 52* (S). SANTA CATARINA: Campo dos Padres, Bom Retiro, *Reitz 2350* (US), *L. B. Smith & Klein 7852* (US); Lages, *Sehnem 5507* (A), *L. B. Smith & Reitz 10101* (US), *Spannagel 108* (S). RIO GRANDE DO SUL: *Jürgens 270* (F, MO, US).

Holttum (1981, p. 471) uses the epithet var. *polypodioides* (Sw.) Conant. However, the suggested combination at varietal rank for the epithet *polypodioides* was never made.

In addition to the diagnostic characters in the key, subsp. *polypodioides* often has the pinnule apices more attenuated and serrated than in subsp. *capensis*.

Alsophila capensis subsp. *polypodioides* has apparently hybridized with *A. sternbergii*. Reproduction of a segregate has become stabilized via allohomoploidy (see Conant & Cooper-Driver, 1980; Holttum, 1981), resulting in *A. setosa*.

Species 14–30 include 17 of the 18 recognized by Gastony (1973; as species of *Nephelea*); full descriptions and illustrations can be found in his revision. Citations of types for new combinations are from Gastony (1973). *Nephelea concinna* has an intermediate leaf architecture similar to that of other hybrids, and its extreme morphological variability indicates that its reproduction has not become stabilized. It is listed with the other hybrids at the end of the Systematic Treatment.

14. **Alsophila auneae** Conant, nom. nov.

Cyathea pubescens Kuhn, Linnaea **36:** 164. 1869. *Nephelea pubescens* (Kuhn) Tryon, Contr. Gray Herb. **200:** 40. 1970, not *Alsophila pubescens* Baker *in* Hooker & Baker, Synopsis Fil. ed. 2. 456 (= *Trichipteris pubescens* (Baker) Tryon). TYPE: Jamaica, collector not named but probably *Purdie* in 1843 (holotype, B; isotype, BM). This species is named for my mother, Aune Lepisto Conant. Jamaica.

15. **Alsophila balanocarpa** (D. C. Eaton) Conant, comb. nov.

Cyathea balanocarpa D. C. Eaton, Mem. Amer. Acad. Arts, n.s. **8:** 215. 1860. *Nephelea balanocarpa* (D. C. Eaton) Tryon, Contr. Gray Herb. **200:** 38. 1970. TYPE: Cuba, Oriente, 1859, 1860, *C. Wright 1063* (holotype, YU; isotypes, GH, MO, NY, US). Cuba.

16. **Alsophila grevilleana** (Martius) Conant, comb. nov.

Cyathea grevilleana Martius, Ic. Pl. Crypt. Brasil. 78. 1834. *Nephelea grevilleana* (Martius) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: Jamaica, comm. *Greville* in 1832 (holotype, BR, fragment and photo BM, fragment US). Jamaica.

17. **Alsophila jimeneziana** Conant, nom. nov.

Cyathea crassa Maxon, Contr. U.S. Natl. Herb. **13:** 40. 1909. *Nephelea crassa* (Maxon) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: Dominican Republic, Puerto Plata, Pico de Isabel de Torres, 8 July 1887, *Eggers 2735C* (holotype, US; isotype, US). Not *Alsophila crassa* Karsten, Fl. Columb. **2:** 187. *t. 199.* 1869. This species is named in honor of Dr. José de Jesús Jiménez, Santiago, Dominican Republic, in recognition of his contributions to botany in that country. Hispaniola.

18. **Alsophila fulgens** (C. Chr.) Conant, comb. nov.

Cyathea fulgens C. Chr. Kongl. Svenska Vetenskapsakad. Handl. III. **16:** 14. *t. 1* (*figs. 9–12*). 1937. *Nephelea fulgens* (C. Chr.) Gastony, Contr. Gray Herb. **203:** 104. 1973. TYPE: Haiti, Dép. du Nord, St. Louis du Nord, Morne Chavaray, *Ekman H4721* (holotype, S; isotype, US). Hispaniola.

19. **Alsophila portoricensis** (Kuhn) Conant, comb. nov.

Cyathea portoricensis Kuhn, Linnaea **36:** 163. 1869. *Nephelea portoricensis* (Kuhn) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: Puerto Rico, *Balbis s.n.* (holotype, perhaps B; isotypes, B, fragment NY, P). Puerto Rico.

20. **Alsophila woodwardioides** (Kaulf.) Conant, comb. nov.

Cyathea woodwardioides Kaulf. Enum. Fil. 255. 1824. *Nephelea woodwardioides* (Kaulf.) Gastony, Contr. Gray Herb. **203:** 107. 1973. TYPE: without locality or collector (holotype, LZ, presumably destroyed, fragment "ex Herb. Kaulf. fragm. origin., ohne Standortsangabe," P). Jamaica, Hispaniola, Cuba.

21. **Alsophila tussacii** (Desv.) Conant, comb. nov.

Cyathea tussacii Desv. Mém. Soc. Linn. Paris **6:** 323. 1827. *Nephelea tussacii* (Desv.) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: Jamaica, *De Tussac s.n.* (holotype, P, photos GH, UC, US). Jamaica.

22. **Alsophila setosa** Kaulf. Enum. Fil. 249. 1824.

Nephelea setosa (Kaulf.) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: Brazil, *Chamisso s.n.* (holotype, LZ, presumably destroyed; isotype, B). Southeastern Brazil, Argentina.

23. **Alsophila tryoniana** (Gastony) Conant, comb. nov.

Nephelea tryoniana Gastony, Contr. Gray Herb. **203:** 118. 1973. *Alsophila tryonorum* Riba is *Trichipteris tryonorum* (Riba) Tryon. TYPE: Guatemala, Dept. Zacapa, Sierra de las Minas, *Steyermark 3009* (holotype, F; isotype, US). Guatemala, Nicaragua, Honduras.

24. **Alsophila erinacea** (Karsten) Conant, comb. nov.

Cyathea erinacea Karsten, Linnaea **28:** 453. 1857. *Nephelea erinacea* (Karsten) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: Venezuela, Mérida, *Karsten s.n.* (holotype, probably LE or W; isotype, B). Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia.

25. **Alsophila imrayana** (Hooker) Conant, comb. nov.

Cyathea imrayana Hooker, Sp. Fil. **1:** 18. *t. 9, B.* 1844. *Nephelea imrayana* (Hooker) Tryon, Contr. Gray Herb. **200:** 40. 1970. LECTOTYPE: Dominica, Couliaban Mt., *Imray s.n.* (holotype, K, fragments NY). Lesser Antilles, Venezuela, Ecuador, Panama, Costa Rica.

26. **Alsophila cuspidata** (Kunze) Conant, comb. nov.

Cyathea cuspidata Kunze, Linnaea **9:** 101. 1834. *Nephelea cuspidata* (Kunze) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: Peru, prov. Maynas, February 1831, *Poeppig 2286* (holotype, LZ, presumably destroyed; isotypes, B, P, NY, US). Nicaragua, Costa Rica, Panama, Colombia, French Guiana, Ecuador, Amazonian Brazil, Peru, Bolivia, Paraguay.

27. **Alsophila sternbergii** (Sternb.) Conant, comb. nov.

Cyathea sternbergii Sternb. Fl. Vorwelt **1:** 47. *t. c.* 1820. (Essai Monde Prim. **4:** 52. *t. c.* 1826.) *Nephelea sternbergii* (Sternb.) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: habitat in Brasiliae Capitania Goyaz ad Limoero non procul St. Izidro, *Pohl s.n.* (holotype, PRC or perhaps W; isotypes, BM, BR, PRC). Southeastern Brazil, Paraguay.

28. **Alsophila incana** (Karsten) Conant, comb. nov.

Cyathea incana Karsten, Fl. Columb. **1:** 75. *t. 37.* 1860. *Nephelea incana* (Karsten) Gastony, Contr. Gray Herb. **203:** 137. 1973. TYPE: Colombia, Cundinamarca, *Lindig s.n.* (authentic material (Villeta, 1900 m), LE, P). Not *Alsophila incana* Geert, Rev. Hort. Belg. Étrangère **32:** 242. 1906; **34:** 172, 179. 1908. Neither the figure facing p. 172 nor the apparent date of publication complies with Article 44 of the *International Code of Botanical Nomenclature.* Colombia, Ecuador, Peru, Bolivia, northern Argentina.

29. **Alsophila firma** (Baker) Conant, comb. nov.

Hemitelia firma Baker, J. Bot. **15:** 161. 1877. TYPE: Ecuador, collected in Andes of Quito, August 1875, *Sodiro s.n.* (holotype, K; isotypes, P, US). *Cyathea mexicana* Schlect. & Cham. Linnaea **5:** 616. 1830. *Nephelea mexicana* (Schlect. & Cham.) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: Mexico, Jalapa, *Schiede s.n.* (holotype, B; isotype, BM). Not *Alsophila mexicana* Martius, Ic. Pl. Crypt. Brasil. 70. *t. 45.* 1834 (= *Trichipteris mexicana* (Martius) Tryon). Not *Alsophila articulata* Houlston & Moore, Gard. Mag. Bot. **3:** 332. *fig. 81.* 1852. Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Ecuador.

30. **Alsophila polystichoides** Christ, Bull. Soc. Roy. Bot. Belgique **35**(Mém.): 177. 1896.

Nephelea polystichoides (Christ) Tryon, Contr. Gray Herb. **200:** 40. 1970. TYPE: Costa Rica, "arborescent" pentes boisées au dessus d'Aragon, 600 m, 20 Oct. 1894, *Pittier 9017* (holotype, BR; isotypes, NY, US). Costa Rica, Panama.

HYBRIDS

The following list of hybrids is in geographic order (Puerto Rico, Hispaniola, Cuba, Jamaica). Conant (1975) made a detailed morphological study of no. 33, *Alsophila amintae* × *A. portoricensis* (as *A. dryopteroides* × *Nephelea portoricensis*) and proposed nos. 34, 36, 37, and 38 as putative hybrids. Since then, field work has supplied further evidence for the hybrid origins of nos. 34, 36, and 37 and has disclosed additional hybrids in Puerto Rico (nos. 31, 32) and the Dominican Republic (no. 35). Conant and Cooper-Driver (1980) presented morphological and chemosystematic evidence for the hybrid origins of nos. 31, 32, and 33 and provided an analysis of their population ecology and fertility.

Puerto Rico

31. **Alsophila amintae** Conant × **Alsophila bryophila** Tryon

DISTRIBUTION AND ECOLOGY. Puerto Rico (Cordillera Central, Monte Jayuya). Disturbed cloud forest; 1150 m alt. This hybrid is to be expected on Monte Guilarte, where plants of the two parent species occur together.

REPRESENTATIVE SPECIMENS. **Puerto Rico:** Cordillera Central, Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 1964* (GH), *1966* (F, GH, IJ, K, NY, US), *Conant & Kitfield 2282* (GH).

This hybrid has a short stem, which may be quite slender (as in *Alsophila amintae*) or moderately stout (as in *A. bryophila*). It has pinnate-pinnatifid leaves (as in both parents), which are quite pubescent and are gradually narrowed at the base to one to a few pairs of subaphlebioid basal pinnae. Some plants (e.g., *Conant 1964, Conant & Kitfield 2282*) have coriaceous leaves similar to those of *A. bryophila,* while others (e.g., *Conant 1966*) have more herbaceous leaves as in *A. amintae.* All have abundant trichomes, a character of *A. bryophila,* and on the undersurface of the pinna-rachis all have bicolorous, lanceolate scales with a single apical seta, a character of *A. amintae.* One collection from Monte Jayuya, *Conant & Kitfield 2281* (GH), is similar in size to plants of this hybrid, is quite pubescent, and has subaphlebioid basal pinnae, but it lacks the bicolorous, lanceolate scales with a single apical seta.

32. **Alsophila bryophila** Tryon × **Alsophila portoricensis** (Kuhn) Conant

DISTRIBUTION AND ECOLOGY. Puerto Rico (Sierra de Luquillo, Cordillera Central). Along streams and trails in cloud forest; 725–1200 m alt. This hybrid is to be expected in the Sierra de Cayey, where plants of the two parent species frequently occur together.

REPRESENTATIVE SPECIMENS. **Puerto Rico.** Sierra de Luquillo: *Conant 1562* (F, GH, HB, Herb. EVFS, Herb. JBRMM, IJ, NY, SV, US), *1650* (GH), *1652* (F), *1653* (US), *1654* (NY). Cordillera Central: Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 1759* (GH, NY, US), *1788* (F, GH, Herb. EVFS, Herb. JBRMM, IJ, SV), *1789* (GH, NY, US), *1814* (GH, K, US), *Conant & Kitfield 2288* (GH, Herb. EVFS, Herb. JBRMM, IJ, SV); Monte Guilarte, W of Adjuntas, ca. 85 km WSW of San Juan, *Conant 1907* (GH, NY, US), *1919* (K, NY, SV, US).

Plants of this hybrid are tall and stout stemmed, as are both *Alsophila bryophila* and *A. portoricensis,* and vigorous ones may reach a height of 12 meters. The stem of the hybrid is usually quite spiny. There is a continuous gradation of leaf morphology in hybrids between these species, suggesting that extensive backcrossing and/or F_2 segregation is occurring (see Conant & Cooper-Driver, 1980). Some plants (e.g., *Conant 1698, 1711, 1774, 1780, 1840,* and *1907,* and *Conant & Kitfield 2287* and *2294*) are close to *A. portoricensis,* while others (e.g., *Conant 1789, 1790, 1791, 1792,* and *1958,* and *Conant & Kitfield 2323*) are quite close to *A. bryophila.* Still other plants (e.g., *Conant 1562, 1696, 1716, 1779, 1788, 1814, 1850,* and *1919*) are definitely intermediate between the parent species.

In general, leaves of the hybrid tend to be longer and narrower and to have longer, narrower pinnae than leaves of *Alsophila portoricensis.* The pinnae of *A. portoricensis* have a width/length quotient of 0.31–0.48, whereas those of *A. bryophila* have a quotient between 0.09 and 0.13. Plants agreeing with the parental species in other characters and with width/length quotients between these ranges are most likely hybrids.

Other diagnostic characters of this hybrid are pubescent indusia and short spines on the petiole (both as in *Alsophila portoricensis*), and moderate to dense pubescence on the axes and veins and a "droop-tip" type of vernation (as in *A. bryophila*).

A series of juvenile plants collected on the El Toro Trail in the Sierra de Luquillo, *Conant 1742, 1744, 1746, 1747,* and *1753,* undoubtedly represent natural F_2 segregates. They closely resemble juvenile plants of *Alsophila bryophila* in leaf shape and dissection, but bear spines on their petioles—a character unmistakably inherited from *A. portoricensis* (see Conant & Cooper-Driver, 1980).

33. **Alsophila amintae** Conant × **Alsophila portoricensis** (Kuhn) Conant

Alsophila dryopteroides (Maxon) Tryon × *Nephelea portoricensis* (Kuhn) Tryon, Rhodora **77**: 442. 1975.

DISTRIBUTION AND ECOLOGY. Puerto Rico (Cordillera Central). Shaded palm forest; 1000–1200 m alt.

REPRESENTATIVE SPECIMENS. **Puerto Rico.** Cordillera Central: Monte Jayuya, near Cerro de Punta, ca. 65 km WSW of San Juan, *Conant 680* (GH, NY, US), *687* (F, GH, Herb. EVFS, IJ, NY, RPPR, US, USD), *1705* (GH, NY, US), *1954* (SV), *1960* (K), *1961* (US), *1963* (NY), *Conant & Kitfield 2259, 2260, 2316, 2321* (GH); Monte Guilarte, W of Adjuntas, ca. 85 km WSW of San Juan, *Conant 1906* (F, GH, HB), *1915* (GH, K, NY, US).

Plants of this hybrid grow to about 2 meters in height and usually have a slender stem armed with short spines; they are similar in size and overall appearance to *Alsophila amintae.* They can be distinguished from this species by several characteristics inherited from *A. portoricensis*: spiny stems and petioles, bipinnate-lobed to bipinnate-pinnatifid leaves, and presence of marginally setate, acaroid scales on the undersurface of the pinna-rachis. A few vigorous hybrid plants (e.g., *Conant 1915, 1959, 2291,* and *2292*) have a rather stout stem and are unusually spiny.

In this hybrid gradation of leaf morphology is not continuous between the parental species. All plants are much more similar to *Alsophila amintae* than to *A. portoricensis,* suggesting either that backcrossing occurs only in the direction of *A. amintae* or that this hybrid has a stable reproduction and is reproducing itself. Population studies by Conant and Cooper-Driver (1980) have shown that in one area this hybrid is more abundant than its parents and appears to be forming small colonies.

34. **Alsophila brooksii** (Maxon) Tryon × **Alsophila portoricensis** (Kuhn) Conant

Alsophila brooksii (Maxon) Tryon × *Nephelea portoricensis* (Kuhn) Tryon, Rhodora 77: 451. 1975.

DISTRIBUTION AND ECOLOGY. Puerto Rico (vicinity of Indiera Fria, near Maricao). Shaded ravines along streams; 760–850 m alt.

REPRESENTATIVE SPECIMENS. **Puerto Rico**: Indiera Fria, near Maricao, *Britton, Cowell, & Brown 4520* (NY), *Conant 1677* (GH, Herb. EVFS, Herb. JBRMM, IJ, NY, SV, US), *Conant & Wells 3446, 3447* (GH).

The prostrate stem, long petioles, and long, narrow pinnae of this hybrid are characters of *Alsophila brooksii,* while the stoutness of the stem, the spines on the stem and petioles, and the bipinnate-pinnatifid leaves are derived from *A. portoricensis.* All collections of this plant are from the vicinity of Indiera Fria, near Maricao on the western end of Puerto Rico, where *A. brooksii* and *A. portoricensis,* the only two species of *Alsophila* in this region, commonly occur together.

Hispaniola

35. **Alsophila brooksii** (Maxon) Tryon × **Alsophila fulgens** (C. Chr.) Conant

DISTRIBUTION AND ECOLOGY. Dominican Republic (vicinity of San Francisco de Macorís). Cloud forest; 725 m alt.

REPRESENTATIVE SPECIMENS. **Dominican Republic.** PROV. DUARTE. Vicinity of San Francisco de Macorís: Los Bracitos, *Abbott 2031* (GH (in part), US); Loma Quita Espuela, *Conant 2113* (GH, Herb. EVFS, IJ, SV, US), *2114* (GH, Herb. JBRMM), *2140* (GH, NY).

This hybrid has a short, prostrate to decumbent stem, long petioles, and long, narrow leaves and pinnae. The dissection of the lamina varies from bipinnate-lobed to bipinnate-pinnatifid—a character that, when combined with the long narrow pinnae, is characteristic of hybrids between pinnate-pinnatifid and bipinnate-pinnatifid species. Plants of this hybrid were growing with *Alsophila brooksii* and *A. fulgens* at Loma Quita Espuela, near San Francisco de Macorís. The short, prostrate stem, long petioles, and long, narrow leaves indicate that *A. brooksii* is one parent. The complexity of the lamina of the hybrid suggests that the second parent is one of the bipinnate-pinnatifid species (*A. fulgens, A. jimeneziana,* or *A. woodwardioides*). Although *A. fulgens* was the only bipinnate-pinnatifid species encountered in the immediate vicinity of the hybrid plants and its characters are consistent with the requirements of the second parent, confirmation of the second parent must await further detailed morphological and chemosystematic analyses.

36. **Alsophila minor** (D. C. Eaton) Tryon × **Alsophila woodwardioides** (Kaulf.) Conant

Cyathea irregularis Brause, pro species, *in* Urban, Symb. Antill. 7. 155. 1911. TYPE: Dominican Republic, Prov. La Vega, prope Constanza infra Valle Nuevo, *Türckheim 3212* (holotype, B, photos GH! and US!; isotype, NY!).

DISTRIBUTION AND ECOLOGY. Dominican Republic (La Vega and Barahona provinces). Cloud forest; 1650 m alt.

REPRESENTATIVE SPECIMENS. **Dominican Republic.** LA VEGA: between Constanza and Valle Nuevo, ca. 16 km S of Constanza, *Conant 2026* (GH), *2029* (F, GH, NY), *2031* (GH, Herb. EVFS, Herb. JBRMM, IJ, K, NY, SV, US). BARAHONA: Montiada Nueva, *Liogier 14251* (Herb. JBRMM).

Plants of this hybrid are tall, stout stemmed, and with adventitious buds at the base and spines on the stem and petioles; in these characters they resemble *Alsophila woodwardioides.* The leaves and pinnae, however, are longer, narrower, and less dissected than in this species and approach the shape of leaves of *A. minor.* The hybrids also have the unusual "droop-tip" type of vernation otherwise found in Hispaniola only in *A. minor.*

Several plants of this hybrid (*Conant 2026, 2029, 2031*) that were growing with *Alsophila minor* and *A. woodwardioides* at the edge of the forest (1650 m alt.; 16 km S of Constanza) are quite similar to Türckheim's original collection.

37. **Alsophila hotteana** (C. Chr. & Ekman) Tryon × **Alsophila woodwardioides** (Kaulf.) Conant

Cyathea confinis C. Chr., pro species, Kongl. Svenska Vetenskapsakad. Handl. III. **16**(2): 13. 1937. TYPE: Haiti, Dép. du Sud, near Jérémie, Massif de la Hotte, Morne l'Étang, *Ekman H10382* (holotype presumably at S, not seen; isotypes, US (2 sheets)!). *Alsophila confinis* (C. Chr.) Tryon, pro species, Contr. Gray Herb. **200:** 29. 1970.

Alsophila hotteana (C. Chr. & Ekman) Tryon × *Nephelea* sp. *in* Conant, Rhodora **77:** 452.

DISTRIBUTION AND ECOLOGY. Haiti (Massif de la Hotte). Cloud forest; 1200 m alt.

REPRESENTATIVE SPECIMEN. **Haiti.** DÉP. DU SUD: Massif de la Hotte, above Sapoti, Pic Macaya, *Barrington 545* (GH).

This hybrid has been collected only once since Ekman's original collection. The stem of *Alsophila hotteana* × *A. woodwardioides* is erect, grows to about 2 m tall, and is rather slender. The small spines on the stem and petioles of this hybrid are characters inherited from *A. woodwardioides*. Characters intermediate between *A. woodwardioides* and *A. hotteana* are the bipinnate-lobed leaves and the subcyatheoid indusium. This hybrid is similar to *A. hotteana* in having either no or few trichomes on the pinna- and pinnule-rachises. Leaves of this hybrid have the typical circinate vernation, as does *A. woodwardioides*. Although the vernation of *A. hotteana* is not known, it is presumably also of this type.

Cuba

38. **Alsophila balanocarpa** (D. C. Eaton) Conant × **Alsophila woodwardioides** (Kaulf.) Conant

Nephelea balanocarpa (D. C. Eaton) Tryon × *Nephelea woodwardioides* (Kaulf.) Gastony, Rhodora **77:** 452. 1975.

DISTRIBUTION AND ECOLOGY. Cuba (Oriente). Presumably in cloud forest.

REPRESENTATIVE SPECIMENS. **Cuba.** ORIENTE: *León, Clément, & Roca 10533* (NY), *Hioram & Clément 6377* (US).

Like other hybrids between pinnate-pinnatifid and bipinnate-pinnatifid species, this hybrid has an intermediate lamina dissection and pinna width/length quotient. *Alsophila woodwardioides* is one parent since it is the only bipinnate-pinnatifid *Alsophila* in Cuba. Three pinnate-pinnatifid to bipinnate species of the genus (*A. brooksii, A. balanocarpa,* and *A. minor*) occur in Cuba, but only the latter two are common. *Alsophila balanocarpa* and *A. minor* are readily separable (even with incomplete or fragmentary specimens) due to the presence of abundant conspicuous, tiny, antrorse, golden trichomidia on the veins of *A. balanocarpa*. These trichomidia are inconspicuous or absent in *A. minor* but abundant on the veins of the hybrid, indicating that *A. balanocarpa* is probably the second parent (the veins of *A. woodwardioides* lack these trichomidia).

Jamaica

39. **Alsophila auneae** Conant × **Alsophila tussacii** (Desv.) Conant

Cyathea arborea var. *concinna* Jenman, J. Bot. **19:** 52. 1881. TYPE: Jamaica, 1879, *Jenman 2* (holotype, K, not seen). *Cyathea concinna* (Jenman) Jenman, pro species, Bull. Bot. Dept. **26:** 4. 1891. *Nephelea concinna* (Jenman) Tryon, pro. species, Contr. Gray Herb. **200:** 38. 1970.

DISTRIBUTION AND ECOLOGY. Jamaica (Blue Mountains). Cloud forest; 1000–1700 m alt.

REPRESENTATIVE SPECIMENS. **Jamaica.** PORTLAND: *Gastony 24* (GH), *Gastony & Gastony 951* (GH), *Riba 198* (GH). PORTLAND–ST. THOMAS: *Maxon 10039* (GH).

Gastony (1973) questioned the status of *Nephelea concinna* as a species and suggested that the taxon might represent a hybrid between *Alsophila auneae* and *A. tussacii* (as species of *Nephelea*). He noted that it was similar to *A. tussacii* in its stem, croziers, and indument, and that it was separated mainly on the bases of its less complex lamina and its tendency to have reduced basal pinnae (two features attributable to *A. auneae,* which has a pinnate-pinnatifid lamina and subaphlebioid basal pinnae).

The range of lamina dissection seen in specimens of *Nephelea concinna* is similar to that in hybrids between the Puerto Rican species *Alsophila bryophila* and *A. portoricensis* (see Conant & Cooper-Driver, 1980, *fig. 3,* p. 1277). Gastony (1973, p. 115) noted that the spores and sporangia of *N. concinna* appeared "quite normally developed" (see also Gastony & Tryon, 1976, *fig. 116,* p. 756 for a scanning electron micrograph of the spore of *N. concinna*), suggesting that it is a fertile hybrid. Morphological variability is to be expected among the segregates and backcrosses of fertile F_1 hybrid plants.

DUBIOUS NAMES

Cyathea conquisita Jenman, J. Bot. **20:** 324. 1882. TYPE: Jamaica, *Wilson 134* (holotype, BM!, fragment US!, photo GH!).

Cyathea pendula Jenman, *ibid.* TYPE: Jamaica, *Wilson 16* (holotype, BM!, fragment US!, photo GH!). *Cyathea conquisita* and *C. pendula* probably belong to the same taxon but are known only from single fragmentary specimens inadequate for critical determination.

Cyathea jamaicensis Jenman, *ibid.*: 323. TYPE: Jamaica, *Wilson 686* (holotype, BM, not seen, fragments NY!, US!, photo GH!; isotypes, GH!, K!). This presumed hybrid (Conant, 1975) is known only from Wilson's type collection at Mansfield, near Bath, Jamaica. Although it is similar in leaf architecture to other hybrids between pinnate-pinnatifid and bipinnate-pinnatifid species, the single fragmentary specimen is inadequate for taxonomic determination and its parentage remains unknown.

Alsophila grevilleana Wallich, Num. List, no. 7075. 1829. Nomen nudum.

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INDEX TO NUMBERED EXSICCATAE

The numbers in parentheses refer to the corresponding species and subspecies in the text. Not all exsiccatae are listed under "Representative Specimens" in the text.

Britton & Cowell 4223 (7).

Britton, Cowell, & Brown 4520 (34).

Buchanan 519 (13a).

Burchell 5862 (13a).

Chase 5671 (13a).

Clément 461, 3976, 6732 (6).

Conant 595, 598 (2); *599* (33); *676, 677* (7); *678* to *680* (33); *681* to *683* (2); *687* (33); *688* (5); *689, 690* (2); *1562* (32); *1564, 1565, 1584* to *1595, 1599* to *1604* (5); *1620* (2); *1621, 1624* (33); *1625, 1628, 1647* (5); *1650, 1652* to *1654* (32); *1656* (7); *1677* (34); *1681, 1683* to *1685* (7); *1696, 1698* (32); *1699, 1700* (2); *1702* (5); *1703* to *1707* (33); *1711* to *1714, 1716, 1718, 1725* (32); *1726, 1727* (5); *1739* to *1744, 1746, 1747, 1752, 1753* (32); *1754* (5); *1756* (32); *1757* (16); *1758, 1759* (32); *1760, 1762* to *1766* (33); *1767* (2); *1774* (32); *1775* (5); *1776* (32); *1777* (33); *1778* to *1780* (32); *1782* to *1784, 1786, 1787* (33); *1788* to *1792* (32); *1793* to *1807* (33); *1808* (2); *1809* (33); *1811* (5); *1812* (2); *1813, 1814* (32); *1815* to *1825, 1827, 1828, 1832, 1833, 1835* to *1838* (33); *1840, 1841* (32); *1843* to *1846, 1849* (33); *1850* (32); *1851* to *1862, 1879* to *1883, 1886* to *1889, 1891, 1892* (2); *1896* to *1899, 1901, 1903, 1904* (5); *1906* (33); *1907* (32); *1908, 1915* (33); *1918* (5); *1919* (32); *1921* (5); *1922* (2); *1923* to *1933* (7); *1953* (2); *1954, 1955* (33); *1956, 1957* (2); *1958* (32); *1959* to *1961* (33); *1964, 1966* (31); *1968, 1970* to *1981, 1983* to *1988, 1990* to *1996* (33); *1997* (32); *1998* to *2000* (33); *2003* (5); *2014* to *2023* (8); *2024* (6); *2025* (8); *2026, 2029, 2031* (36); *2046* to *2049* (6); *2050* (8); *2051* to *2063* (6); *2102* to *2104* (8); *2113, 2114* (35); *2115* to *2138* (3); *2140* (35); *2141* (7); *2145* (2); *2146* to *2148* (5); *2152, 2173, 2179* to *2181* (2).

Conant & Kitfield 2253 to *2255* (5); *2256* to *2258* (2); *2259, 2260* (33); *2261* (32); *2262* to *2268, 2270* to *2272* (5); *2273* to *2277* (2); *2278* to *2280* (33); *2281, 2282* (31); *2283* to *2286* (5); *2287, 2288* (32); *2290* to *2292* (33); *2293* to *2297* (32); *2299* (5); *2301* (2); *2302* to *2308* (5); *2309, 2310, 2312, 2313* (2); *2314* to *2316* (33); *2318, 2319* (32); *2320* (5); *2321* (33); *2323* (32); *2325* to *2341* (5).

Conant & Wells 3446, 3447 (34).

Cowles 408 (5).

Cuatrecasas 13396 (9).

Cummings 315 (13a).

Dummer 1Dt (13a).

Eggers 5171 (6); *5252* (6, in part).

Ekman H1140 (6); *H2874* (7); *H3728* (3); *H3864, H3864a, H3864b* (7); *3873, 4041* (6); *H5243* (4); *H5334* (6); *H6339* (8); *6854* (6); *H10382* (37); *H10383* (4); *H11195* (7); *H11515* (7); *H11628, H11815* (8); *H12009* (6); *H12277* (3); *H12278* (7); *H13211, H14057* (8); *14545* (6).

Engel 138 (11).

Ewan 16695 (10).

Fisher & Schweickerdt 48 (13a).

Flanagan 1531 (13a).

Fuertes 1547 (6).

Gardner 5954 (13b).

Gastony 12 (5); *24* (39).

Gastony & Gastony 951 (39).

Gastony, G. C. Jones, & Norris 321 (6); *384* (8); *436, 629* to *636* (6); *557* (8); *728, 736* (6).

Glaziou 3583, 4400 (13b).

Harris 7322 (1).

Hart 13, 2838 (1).

Hellwig 408 (12).

Hernández & Sharp X336 (12).

Hess 182, 349, 7008 (7).
Hess & Stevens 2951 (5).
Hialewstri 52 (13b).
Hioram 4107 (6, in part).
Hioram & Clément 6377 (38).
Hioram & Maurel 4107, 5009 (6).
Holdridge 2175 (4).
Howard 15722, 15725, 16376 (5).
Howard & Howard 8545 (3, 6); *8563* (6).
Howard & Nevling 15740, 16004, 16014 (5).
Howard et al. 15645 (5).
Jenman 2 (39).
Jiménez 3968, 4013, 4551 (8).
Jiménez & Marcano 3062 (3).
H. Johnson 959 (12).
G. N. Jones 10966, 11009 (5).
G. C. Jones & Norris 1129 (6).
Judd 1223 (6); *1380, 1386* to *1389* (3); *1390* (6); *1391, 1393, 1400, 1404* (3); *1521, 1523, 1524* (8).
Judd, Liogier, & Liogier 1087 (6).
Jürgens 147, 270 (13b).
J. P. 42 (1).
Kennedy 1853 (13a).
Lavastre 2014, 2016 (8).
León, Clément, & Roca 10533 (38).
León & Ekman 11151 (6).
Liogier 11482 (7); *14251* (36); *14806* (3); *14807, 16071* (8); *17067* (6).
Liogier & Liogier 19943 (3).
Liogier, Liogier, & Melo 23490 (7).
Little 21606 (5).
Luetzelburg 211a, 18905 (13b).
Maxon 2791 (1); *4134* (6); *4474* (7); *10039* (39).
Molina 10253, 10674, 13619, 22104, 23405 (12).
Molina, Burger, & Wallenta 16749 (12).
Molina et al. 16974 (12).
Morton 6932, 7173 (12); *9346, 9362* (6).
Morton & Acuña 3193 (6).
Münch 139 (12).
Nock 107 (1).
Pennell 9695 (11).
Peter 28018 (13a).
Purpus 6768, 6769 (12).
Reitz 2350 (13b).
Riba 198 (39).
Rodin 1190 (13a).
Rogers 17502 (13a).
Roig 6731 (6).
Rudatis 1551 (13a).
Sargent 404, 636 (7); *3141* (2).
Scamman 6519 (5).
Schelpe 6181 (13a).
Sehnem 5507, 6327 (13b).
Seifriz 5 (8).
Shafer 3305, 3632 (5); *4154, 4454* (6); *8033, 8224* (6, in part).

Sim et al. 1573 (13a).
Sintenis 1480 (5).
J. Smith 10 (13a).
L. B. Smith & Klein 7852 (13b).
L. B. Smith & Reitz 10101 (13b).
Spannagel 108 (13b).
Spruce 5363 (10).
Standley 4826, 13550 (12).
Standley & Williams 735, 738 (12).
Steyermark 42538, 42790, 48924 (12).
Stone & Broome 2814 (12).
Stone & Stone 2706 (12).
Stübel 1007 (10).
Tidmarsh 2 (13a).
Tillet 636-4 (12).
Tryon & Tryon 6347, 6381 (13a).
Türckheim 845, II2027 (12); *3076, 3076b* (8); *3115* (6); *3213* (36).
Underwood 1355 (1).
Vainio 33210 (13b).
White 1969240 (11).
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Wilson 170 (5).
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DEPARTMENT OF NATURAL SCIENCES
LYNDON STATE COLLEGE
LYNDONVILLE, VERMONT 05851

THE GENERA OF ALISMATACEAE IN THE SOUTHEASTERN UNITED STATES[1]

George K. Rogers

ALISMATACEAE Ventenat, Tabl. Règne Vég. **2**: 157. 1799, "Alismoideae," nom. cons.

(Water-Plantain Family)

Glabrous or subglabrous, usually perennial, most often emergent herbs of wet places, the petioles and other organs with air spaces traversed by diaphragms. Vegetative axes condensed erect stems, sympodial rhizomes, axillary stolons, and terminal pseudostolons. Vessels confined to the roots, with simple or scalariform perforations. Epithelium-lined laticifers in most organs of most taxa, rare in roots. Single or clustered crystals often present (especially in the leaves), these usually small rod-shaped styloids or rhomboids, sometimes crystal sand, occasionally raphides (these or "Nädelchen" reported in *Alisma, Echinodorus,* and *Sagittaria*), or infrequently druses (reported in *Sagittaria* among our genera). Leaves basal [rarely cauline], spirally arranged or spirodistichous (infrequently distichous), often with hydropoten,[2] highly variable and environmentally plastic, submersed, floating, or (usually) erect and emergent, usually petiolate, the blade linear (especially in submersed forms) to cordate or sagittate, the principal nerves parallel with the margins and tending to converge at the apex; stomata usually paracytic, sometimes tetracytic, [rarely otherwise]; petioles with broadened, open, sheathing bases. Intravaginal scales

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Thanks are due Carroll Wood for his careful review of the manuscript. Translation of literature from Chinese by Shiu-Ying Hu was a valuable contribution. Donna Rogers, my wife, translated literature from French and participated adeptly in troubleshooting the manuscript. Figure 1 is the work of Laszlo Meszoly, who used materials of *Alisma subcordatum* collected and dissected by the author. Karen S. Velmure drew Figure 2, for which dissections were prepared by K. R. Robertson and C. E. Wood.

[2] This seldom-encountered term refers to groups of specialized, flattened cells on submersed leaves and petioles; these are involved in the uptake of salts and facilitate the passage of water.

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usually present. Inflorescences terminal (vegetative growth proceeding by a precociously developed meristem in the axil of the leaf immediately beneath the inflorescence), usually [spikes,] racemes, or panicles, sometimes umbelliform, sometimes lax, even horizontal, the bracts in (pseudo-)whorls of 3 at the nodes, sometimes with vegetative buds mixed with or completely replacing flowers. Flowers and branches borne either in condensed, sympodial, bostrycoid complexes (usually in *Alisma* and *Echinodorus*) or singly in axils of bracts (with exceptions, *Sagittaria*). Flowers regular, hypogynous, perfect or imperfect, with 3 imbricate, green sepals, and 3 imbricate, usually white [sometimes reddish or yellow], delicate, ephemeral petals [these infrequently reduced or absent]. Stamens [3–]6 to many, with 2-locular, mostly extrorsely dehiscing anthers; pollen grains more or less spherical or polyhedric, pantoporate (ours), with granules or spinules on the sexine, 3-nucleate when released. Gynoecium of [3 to] many free carpels (sometimes slightly connate at the base), these usually laterally compressed, on a flat or rounded receptacle, each carpel with a terminal or adaxial style and 1 [or more in *Damasonium*] adaxial-basal, anatropous or variably bent, apotropous [or epitropous] ovule. Fruits achenes [or follicles in *Damasonium*], usually with variously developed longitudinal ridges; seed with a thin integument, without endosperm; embryo U-shaped with the 2 tips toward the base, the radicular end thickened, germination epigeal. TYPE GENUS: *Alisma* L.

Excluding the three genera of Limnocharitaceae Takhtajan, about 12 genera of temperate and tropical regions, with most species in the Northern Hemisphere. The genera are typically small, mostly with one to 10 species, except *Echinodorus* and *Sagittaria,* which together may account for over 80 species and which clearly will expand with further exploration of the tropics. This estimate, based largely on the attention focused on those two genera in recent years by Rataj, indicates that the total number of species in the family is considerably larger than the 70–100 estimated by most authors. Ranges of four genera extend into the continental United States, three are found in the Southeast, and *Damasonium californicum* Torrey (*Machaerocarpus californicus* (Torrey) Small) occurs in northern California, Oregon, western Nevada, and southwestern Idaho.

In the monocotyledonous families to which Engler's name Helobiae is still often applied (*cf.* Alismatidae of some recent authors), the Alismataceae are usually placed near the Hydrocharitaceae, Butomaceae (here regarded as monogeneric), and Limnocharitaceae, these four making up the Alismatales of Takhtajan (1980) and of Thorne (who, however, did not recognize the Limnocharitaceae at the familial level). Cronquist excluded the Hydrocharitaceae from this order, which is even more restricted in the scheme of Dahlgren & Clifford, in which the Alismataceae (including the Limnocharitaceae) alone comprises the Alismatales.

The Butomaceae differ from the Alismataceae most saliently in their subpetaloid calyces, persistent petals, exclusively linear leaves, lack of secretory canals, straight embryos, uniaperturate pollen, monosporic embryo sacs, numerous ovules scattered on laminar placentae, and uniformly follicular fruits.

Often included in the Butomaceae, the Limnocharitaceae agree with that family in having follicular fruits and many ovules on laminar placentae, but resemble the Alismataceae anatomically, in all of the other characters listed above, and in other ways. (The Limnocharitaceae may differ from both the Alismataceae and the Butomaceae in having stamens develop in a centrifugal pattern; see Sattler & Singh.) The Limnocharitaceae have been included in the Alismataceae by a number of botanists, including Dahlgren & Clifford, Pichon, and Thorne. This position is supported by the intermediacy of two alismataceous genera, *Damasonium* Miller (vasculature of carpels, follicular fruits, number and arrangement of ovules) and *Ranalisma* Stapf (sympodial inflorescences, these atypical of Alismataceae but occurring in Limnocharitaceae).

The flowers of the Alismataceae and related families have often been interpreted as primitive, especially because of their distinct, sometimes numerous, and seemingly spirally arranged stamens and carpels, the latter sometimes remaining open (*Alisma*) and with more or less decurrent stigmas. These features have been taken as indicators of an ancestral position among the helobian monocots and as ties to presumably primitive ranalian dicots, especially the Ranunculaceae and Nymphaeales, some of which (principally the latter) show vegetative resemblances in addition to having flowers of similar appearance. Hutchinson, for example, thought *Ranalisma* (otherwise universally accepted as alismataceous) to be an intermediate link between the Alismataceae and the Ranunculaceae. Affinity with the similarly aquatic Nymphaeales was advocated by Takhtajan (1969). However, the accumulated anatomical, embryological, developmental, and morphological evidence has shown the Alismataceae to be specialized in several ways and contradicts close affinity with the Ranales. (For a concise discussion of the relationship with the Ranunculaceae, see Tomlinson; see also Dahlgren & Clifford; Eames; Eckardt; Maheshwari, 1964; Meyer, 1932; Sculthorpe, pp. 279, 280; Stant; and Thorne, pp. 97, 98.)

In this connection, in a recent series of papers particular attention has been paid to the nature of the androecium and gynoecium. Unlike the spirally arranged but superficially similar flowers of Ranales, the alismataceous flower appears to be fundamentally trimerous. According to Sattler & Singh, this trimery is unlike that found in some Ranales ("Magnoliidae"). Unlike those of the putatively related dicots, the three petals and first six stamens in most genera of Alismataceae arise in a (pseudo?)whorl of three complexes, each of these a petal primordium and an antipetalous stamen-pair. Each complex usually originates as a single protrusion termed a "CA primordium." Primordia for carpels, too, arise in variable, basically trimerous patterns. That additional stamens and carpels in certain genera are secondarily superimposed in nonspiral arrangements on the originally trimerous plan during development has led to the view that their elaboration is phylogenetically secondary, not primitive. (See Leins & Stadler; Sattler & Singh; Singh & Sattler, 1972, 1973, 1977.)

Pichon's division of the Alismataceae *sensu lato* into two tribes and 10 subtribes on the basis of floral characters was not supported by Argue (1976), who found that pollen morphology, in correlation with base chromosome numbers and other characters, points to very different (informal) generic groups.

Punt & Reumer in turn objected to Argue's categories, leaving the matter of infrafamilial subdivisions unsettled.

Leaves are highly variable in the Alismataceae, with their form often plastic in response to water depth and such factors as light intensity and stored food reserves. Submersed (and juvenile) leaves tend to be linear, those borne out of water to have variably expanded blades, and floating leaves to be intermediate. The parts of this range expressed in different taxa are not constant: leaf shape appears to be more or less genetically fixed in connection with habitat in some taxa while varying with environment in others. Heterophylly is discussed further under the individual genera.

Although often described as being of the Scilla-type, development of the megagametophyte in the Alismataceae differs from that of *Scilla* and might better be described as a variant of the Allium-type (see Maheshwari, 1950, p. 98; 1964, p. 89). The megagametophyte is bisporic and is derived from the lower dyad cell, which divides into two chalazal and two micropylar nuclei, the micropylar nuclei each dividing again to yield typically a six-nucleate sac. One or both chalazal nuclei occasionally divide, resulting in megagametophytes with seven or eight nuclei, although suppression of an early division in some cases limits the number of nuclei to five.

Early development of the embryo is of the Caryophyllad-type (as defined by Johansen), the basal cell of the two-celled proembryo enlarging and usually remaining undivided (but see Swamy for a deviating report). Endosperm development of the helobial type is usual; nuclear endosperm has been reported in extraregional genera and repeatedly in species of *Alisma* (Dahlgren, 1928; Frey; Johri, 1936; Pogan, 1965); however, Hasitschka-Jenschke's description of a basal cell in the endosperm of *A. lanceolatum* indicates presence of the helobial type in this genus also. Endosperm is absent from mature seeds. (For embryological details see also Cook, Davis, Dahlgren & Clifford, and Johri.)

Fruits of most Alismataceae, including those in the Southeastern United States, are achenes adapted for aquatic dispersal. Buoyancy is provided by spongy tissue (well developed in *Alisma*) in the pericarp, space between the seed and pericarp (FIGURE 1, i), and resin ducts or "glands" on the lateral faces in *Sagittaria* and *Echinodorus* (and probably by inconspicuous deposits of resin in pericarps of *Alisma*). The surface of the pericarp is (at least when young) resistant to wetting (Arber, 1920; Buchenau, 1903). Flotation for several months has been observed in *Alisma, Echinodorus,* and *Sagittaria,* and maintenance of viability in wet seeds for over a year has been reported for species of *Alisma* and *Sagittaria.* Persistent styles, lateral ribs (*Sagittaria, Echinodorus*), and elaborate protuberances from margins and ribs (some sagittarias) may enhance flotation and/or help the achenes cling to aquatic birds and mammals. That alismataceous achenes are ingested by ducks has often been observed; enhancement of germination by passage through an avian digestive tract has been shown in *Alisma.* The pronounced marginal wing on achenes of species of *Sagittaria* suggests dispersal by wind and probably promotes flotation.

As shown for *Alisma Plantago-aquatica* L. (see particularly Crocker & Davis) but observed in our other genera as well, germination is delayed by mechanical restraint from the seed coat. When this is broken, the radicle penetrates the pericarp through a basal aperture or weak area, then becomes anchored to the substrate by an encircling tuft of hairs (FIGURE 1, l). Food reserves are in the hypocotyl and the cotyledon, which begins photosynthesis early, sometimes while still capped apically by the pericarp. (For further discussion of germination and establishment, see Kaul, 1978. Other references concerned with dispersal and germination of the achenes are Björkqvist, 1967 (see *Alisma*); Ewart; Glück & Kirchner; Holm; Lubbock; Schaumann; and Sculthorpe.)

The fossil history of the Alismataceae was recently reviewed by Daghlian, and the palynological record by Muller.

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WODEHOUSE, R. P. Pollen grains in the identification and classification of plants. VIII. The Alismataceae. Am. Jour. Bot. **23:** 535–539. 1936. [Palynological distinction between *Lophotocarpus* and *Sagittaria* in this paper not upheld by ARGUE, 1976.]

KEY TO THE GENERA OF ALISMATACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Aquatic or palustrine herbs with short, fleshy, erect or horizontal stems sheathed in the bases of usually petiolate leaves, bearing laticifers in most organs; scapes with bracts in apparent verticils of 3, these subtending pedicels or branches; flowers actinomorphic, usually pedicellate, hypogynous, generally with separate parts; perianth of 3 green sepals and 3 usually white, delicate petals; pollen grains polyporate; gynoecium of usually numerous, free carpels, each with an adaxial or terminal style and 1 adaxial-basal ovule; achenes each with a seed bearing a horseshoe-shaped embryo but no endosperm.*

A. Carpels in flat ring; stamens 6; lateral faces of achenes smooth (notched abaxially), without ribs or glands; inflorescences highly branched, paniculate. ..... 1. *Alisma.*

A. Carpels usually on rounded receptacle, not in ring; stamens usually more than 6; lateral faces of achenes usually with 1 or more ribs and/or glands; inflorescences usually either unbranched or branched only at lowest node(s) (*Echinodorus Berteroi* sometimes with panicles as in *Alisma*).

  B. Flowers perfect; inflorescences (usually) with more than 3 flowers per node or umbelliform. .... 2. *Echinodorus.*

  B. Flowers mostly imperfect; inflorescences (usually) with only 3 flowers per node. .... 3. *Sagittaria.*

1. **Alisma** Linnaeus, Sp. Pl. **1:** 342. 1753; Gen. Pl. ed. 5. 160. 1754.

Perennial (or sometimes annual?), glabrous (or nearly so), usually emergent, sometimes submersed [or terrestrial] herbs with rosettes and scapes arising apically from upright, fleshy, bulb-shaped stems, these sometimes forming a series by growth of axillary buds. Leaves highly variable in shape and size, earliest leaves linear, later leaves [sometimes remaining submersed and linear], sometimes floating, then narrow-lanceolate [to linear], blade of emergent or terrestrial leaves elliptic, lanceolate, or ovate, obtuse to acuminate, often cuspidate at the apex, cuneate to cordate at the base, with a conspicuous midvein, the longitudinal nerves diverging from the base of the blade or from the midvein, these interconnected by fairly regularly spaced, parallel, ascending veinlets; petiole usually longer than the blade. Inflorescences 1 to several, erect [sometimes bent in *A. gramineum*], usually taller than the leaves [except on submersed plants], pyramidal, compound panicles with long peduncles and (including the long pedicels) [1 or] 2 or 3(–5) orders of branching, sometimes bearing several hundred flowers, branches and pedicels often mixed, in (pseudo-)whorls of up to 7(–10) [or more] members, with [1–]3–8(–10) nodes, each branch terminating in a flower, this often appearing as a member of an umbelliform cluster; bracts sometimes basally connate, usually subulate to lanceolate (sometimes oblong or ovate). Flowers perfect, with all parts separate (except for varied connate and adnate relationships at their bases). Sepals with hyaline margins, concave, persistent. Petals white (in *A. subcordatum* with a faint yellowish spot near the base when fresh) [to pink or purplish], persisting only 1 day, with entire or slightly wavy margins [to coarsely notched or lobed toward the apex], usually rounded, about as long as or longer than the sepals. Stamens 6, originating as 3 antepetalous pairs (but this relationship not remaining obvious), approximately as long as or longer than the carpels, anthers oblong, elliptic, [or nearly orbicular], filaments broadened toward the base, variably inserted on a ring of tissue above the receptacle, longer than the anthers; pollen grains with granulate, circular (or nearly so) pores, exine tectate, granular to spinulose. Gynoecium a ring of many nearly free carpels on a flat receptacle, these elliptic to obovate (tending to have the adaxial edges straighter than the abaxial edges), or D-shaped, not completely closed at anthesis, with nectaries at the basal adaxial edges, each with an outwardly curled style shorter than the length of the ovary [or the style straight and up to twice the length of the ovary], style inserted at or slightly below the adaxial edge of the broad summit of the ovary [sometimes inserted nearly centrally at the apex to below the middle of the adaxial side]; ovule anatropous or amphianatropous. Achenes ca. [10–]13–20[–35], flattened, obovate to elliptic, sometimes ovate, with rounded apices, the adaxial edges often straight below the remnants of the styles (when present), with 1 or 2 abaxial grooves. Seed flattened, elliptic or obovate-oblong in outline (*A. subcordatum*). LECTOTYPE SPECIES: *Alisma Plantago-aquatica* L., the only one of Linnaeus's original species not removed to other genera; see also J. K. Small, N. Am. Fl. **17:** 43. 1909. (Name ancient, adopted by Linnaeus from Dioscorides.) — WATER-PLANTAIN.

A genus of nine species (as recognized by Björkqvist, 1968) distributed nearly throughout the temperate Northern Hemisphere, extending northward slightly beyond the Arctic Circle (in the Old World), and to the south mostly above the Tropic of Cancer (with some notable transgressions in eastern Asia). *Alisma* only rarely occurs south of the equator: along eastern Africa south to Zimbabwe, in South Africa, Chile, Australia, and New Zealand. *Alisma Plantago-aquatica* accounts for most of these southern outposts, although *A. lanceolatum* With. grows in Australia and Chile. Other than in eastern Africa, these occurrences probably stem from introduction by humans, although this matter is not settled in every case, with some authors especially prone to accept *A. Plantago-aquatica* as possible native to Australia (*cf.* Aston; Björkqvist, 1967; Hultén, 1962; Samuelsson, 1932).

Alisma triviale Pursh and *A. gramineum* Lej. are widespread in the United States, but north and west of the range of the Generic Flora.[3] *Alisma subcordatum* Raf. (*A. Plantago-aquatica* L. var. *parviflora* (Pursh) Torrey, *A. parviflora* Pursh, *A. Plantago-aquatica* L. subsp. *subcordatum* (Raf.) Hultén) grows in every state (except Louisiana?) east of a line connecting Texas, Nebraska, and South Dakota, in southern Canada (perhaps as far west as Saskatoon), and possibly in Arizona and/or in northern Mexico. Rubtzoff reported it (as probably an introduction) in the Yosemite Valley of California.

Alisma subcordatum shares the northern part of its range with the similar *A. triviale*. Although Samuelsson (1933) found intermediates not to be formed between these two species despite the wide geographic overlap (his *A. Plantago-aquatica* subsp. *brevipes* (Greene) Samuels. corresponding to *A. triviale* as used here), other authors (e.g., Hellquist & Crow; Voss, 1972) have noted difficulties in distinguishing them. All of these authors (and Hendricks) included one or both in *A. Plantago-aquatica,* which (as circumscribed by Björkqvist, 1968) is native only to the Old World. That the three are distinct has been advocated by Björkqvist (1968), Fernald (1946), and Pogan (1963, 1964). *Alisma subcordatum* differs from *A. triviale* in being diploid (vs. tetraploid), and in a subtle set of characters probably largely related to the levels of ploidy: *A. subcordatum* has smaller floral parts, pollen grains, stomata, and achenes, and its styles are much shorter than the ovary (vs. about as long). (For detailed comparison see Björkqvist, 1967, 1968; Fernald, 1946; Pogan, 1964.) Not surprisingly, the two species are intersterile.

Alisma is distinguished by its six stamens, its usually complex, highly branched panicles, its many carpels in a flat ring, and its achenes with one or two pronounced abaxial furrows. Although in his recent revision and related studies Björkqvist (1967, 1968) thought *Alisma* to be closest to *Echinodorus, Baldellia* Parl., *Luronium* Raf., *Caldesia* Parl., and *Damasonium,* he (1968, p. 98) found these genera "clearly distinguished from each other by many different morphological characteristics" and, on the basis of crossing experiments, asserted

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[3] Contrary to Hendricks's (p. 484) mention of *Alisma Plantago-aquatica* L. var. *americanum* (= *A. triviale*) in Arkansas, I have identified *Demaree 17866* (GH), a duplicate of the collection he cited, as *A. subcordatum* sensu Björkqvist.

that *Alisma* is "isolated from all other genera by absolute sterility barriers." (However, see *Echinodorus* for discussion of a possible intergeneric hybrid involving *Alisma.*) *Alisma, Caldesia,* and *Limnophyton* Miq. comprised Pichon's subtribe Alismatinae.

Except for the well-known *Alisma Plantago-aquatica,* the several species included in *Alisma* by Linnaeus and Micheli have since been removed to other genera. (Indeed, most species assigned to this genus by the authors who described them have since been placed elsewhere.) Buchenau (1903), in the first revision since that of Micheli, narrowed the generic circumscription by treating *A. Plantago-aquatica* as the sole species. His several varieties and forms of this species reflected the modern circumscription of the genus but not the trend by later botanists toward recognition of multiple species within this assemblage.

Misleading environmental plasticity within species in contrast with relatively low variation in the genus as a whole, coupled with a worldwide distribution and a paucity of type material, has contributed to a confusing lack of accord in the delimitation and nomenclature of species in the three latest revisions. In the first of these, Samuelsson (1932) examined more specimens than his predecessors, recognized six species (one new), and provided particularly useful details of distribution and floral morphology. The revision by Hendricks, who accepted only four species, contributed a unique North American emphasis. His opinions differ radically from Samuelsson's and from Björkqvist's, partly in that his specific delimitations are least correlated with geographic areas. Nomenclatural and other problems with this treatment were outlined by Voss (1958).

A detailed historical survey is available in Björkqvist's revision (1967, 1968), which is buttressed by broadly based and clearly presented anatomical-morphological studies, new experiments to evaluate environmental modification, breeding experiments, and new cytological studies. Nine species emerged as reproductively and morphologically distinct, although as Björkqvist stated, nomenclatural research on these remains incomplete.

Spontaneous hybridization between *Alisma Plantago-aquatica* and *A. lanceolatum* appears to be rare (Björkqvist, 1968; Kloos; Pogan, 1965). Some additional species can be crossed in the laboratory, but the resulting hybrids are sterile or reduced in fertility. Björkqvist detected no sterility barriers between populations of the same species.

Alisma has been the subject of numerous cytological studies, culminating in that by Björkqvist (1968), who reviewed and criticized the considerable previous work. His determinations of chromosome number and morphology are backed by a broad sampling of specimens from each of the species in his revision. The base number in the genus is 7, with *A. Plantago-aquatica, A. gramineum, A. Wahlenbergii* (Holmb.) Juz., *A. subcordatum,* and *A. orientale* (Samuels.) Juz. all being diploids, with $2n = 14$. *Alisma lanceolatum* ($2n = 26$, 28), *A. triviale* ($2n = 28$), and *A. rariflorum* Samuels. ($2n = 26$) are tetraploids. *Alisma canaliculatum* Braun & Bouché is hexaploid ($2n = 42$). However, these figures (as well as the observations on the chromosomal morphology below) are not consistent throughout the cytological literature, with nomenclatural, taxonomic, and technical difficulties contributing to the inconsistencies. As was already mentioned, *A. subcordatum* is not free from such problems. Björkqvist (1968) found $2n = 14$ for this species in 60 specimens. This number was also reported by Baldwin & Speese and Pogan (1963, 1964). Reports of $2n = 28$ by Björkqvist (1961, retracted in 1968), Brown, and Heiser & Whitaker appear to be based upon misidentified material.

The haploid chromosomal sets in each of the nonaneuploid species are fairly uniform: five chromosomes with median or submedian centromeres and two shorter chromosomes with subterminal centromeres. Consolidation between the two short types via reciprocal translocation in tetraploid plants is thought to account for the deficiency in number of chromosomes and the peculiar appearance of one pair in the aneuploids. (For elaboration see Björkqvist, 1968; Castro & Noronha Wagner; Erlandsson; Frey; Hendricks; Mikkola; Oleson; Pogan, 1962, 1967; Sharma; Sharma & Mukherji; Tschermak-Woess; and Wulff.)

Alisma subcordatum grows on wet or periodically flooded soil or in shallow water in bogs, marshes, ditches, ponds, and streams. This species usually does not grow submersed and tends to have the broader forms of leaves, with linear leaves formed only by the seedling. When grown underwater, it produces lax floating leaves with narrow blades (Rhoades). *Alisma gramineum* and *A. Wahlenbergii,* on the other hand, are adapted for growth completely submersed (the former tolerating depths to 4 m, according to Glück & Kirchner) and consequently have predominantly linear leaves. They do not form floating leaves. When these species are grown out of water, the blade is narrow and tapered at both ends. (For additional information on heterophylly in *Alisma,* consult Arber, 1920; Björkqvist, 1967; Glück, 1905; Glück & Kirchner; and Sculthorpe.)

Alisma gramineum (sometimes) and *A. Wahlenbergii* (characteristically) flower and set fruit underwater; the flowers of both have been described as cleistogamous or not opening underwater (Björkqvist, 1968; Wendt).

The most common floral visitors to species of *Alisma* at some European and North American localities have been a variety of dipterans and short-tongued bees. Daumann (1964, 1965; see also Glück & Kirchner, p. 607) found the pollen to be less cohesive than usual for entomophilous plants and demonstrated transfer of pollen by wind. Absence of agamospermy was shown by Björkqvist (1968), who also found every species to be self compatible, a condition of interest in connection with the several disjunct stations for some species.

Since *Alisma gramineum* is particularly well suited to submerged growth, it is useful as an aquarium plant (see Stodola, Wendt). Other species are nuisances as weeds in rice and wild rice (*Zizania*) fields and in drainage ditches (Meeklah & Darwin; Ransom & Oelke; Samuelsson, 1932; Sculthorpe, p. 457). Members of the genus are used only rarely as food (Rickett, Wood *et al.*), probably because of noxious and bioactive compounds in the plants. Several reports indicate toxicity to humans and other mammals, including irritation to human skin (Mitchell & Rook, Wood *et al.*). By far the greatest economic significance of *Alisma* is in medicine, with a history extending from modern pharmacology back to A.D. 200 in China. *Alisma* species (probably mainly *A. orientale*) are cultivated in eastern Asia chiefly for the rhizome, which is sometimes sold sliced or powdered to be used alone or mixed with other drugs. The sundry properties attributed to "*Alismatis Rhizoma,*" too many to list here, are enumerated in Perry, Stuart, and other references.

Most of the pharmacological study concerning *Alisma* involves the ability of the crude drug or compounds isolated from it to diminish concentrations of cholesterol (while altering the balance of other lipids) in the liver and blood of laboratory animals fed certain diets (Imai *et al.*; Kobayashi; Murata *et al.*, 1970a). The lipotropic agent choline was detected by Kobayashi (1960a), but most work has been centered on a group of triterpenes (alisols) that reportedly have diuretic and antiinflammatory activity in rats (Murata *et al.*, 1970a) beyond their effects on metabolism of lipids. Isolation and determination of structures of the alisols have been pursued by Murata and collaborators (see also Kamiya *et al.*). Imai *et al.* refined observations on the hypocholesterolemic activity of alisols (particularly one), compared their efficacies (see also Murata *et al.*, 1970a), discussed the relationship between structures and activities, and mentioned that the alisol they studied most seemed to interfere with the absorption of cholesterol by the intestine.

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2. **Echinodorus** Engelmann in Gray, Man. Bot. 460. 1848.

Annual or perennial, submersed or emergent aquatic herbs, glabrous [or with sparse, single, stellate, or tufted hairs on stems, leaves, petioles, axes of the inflorescence, calyces, and bracts]. Leaves sometimes polymorphic (in our area true of *E. tenellus* and especially *E. Berteroi*), submersed leaves tending to be ribbonlike and emersed leaves petiolate, the blade highly variable, linear to elliptic, lanceolate, deltoid, or cordiform, [retuse or] rounded to long-acuminate at the apex, cuneate to cordate at the base, often with translucent markings,

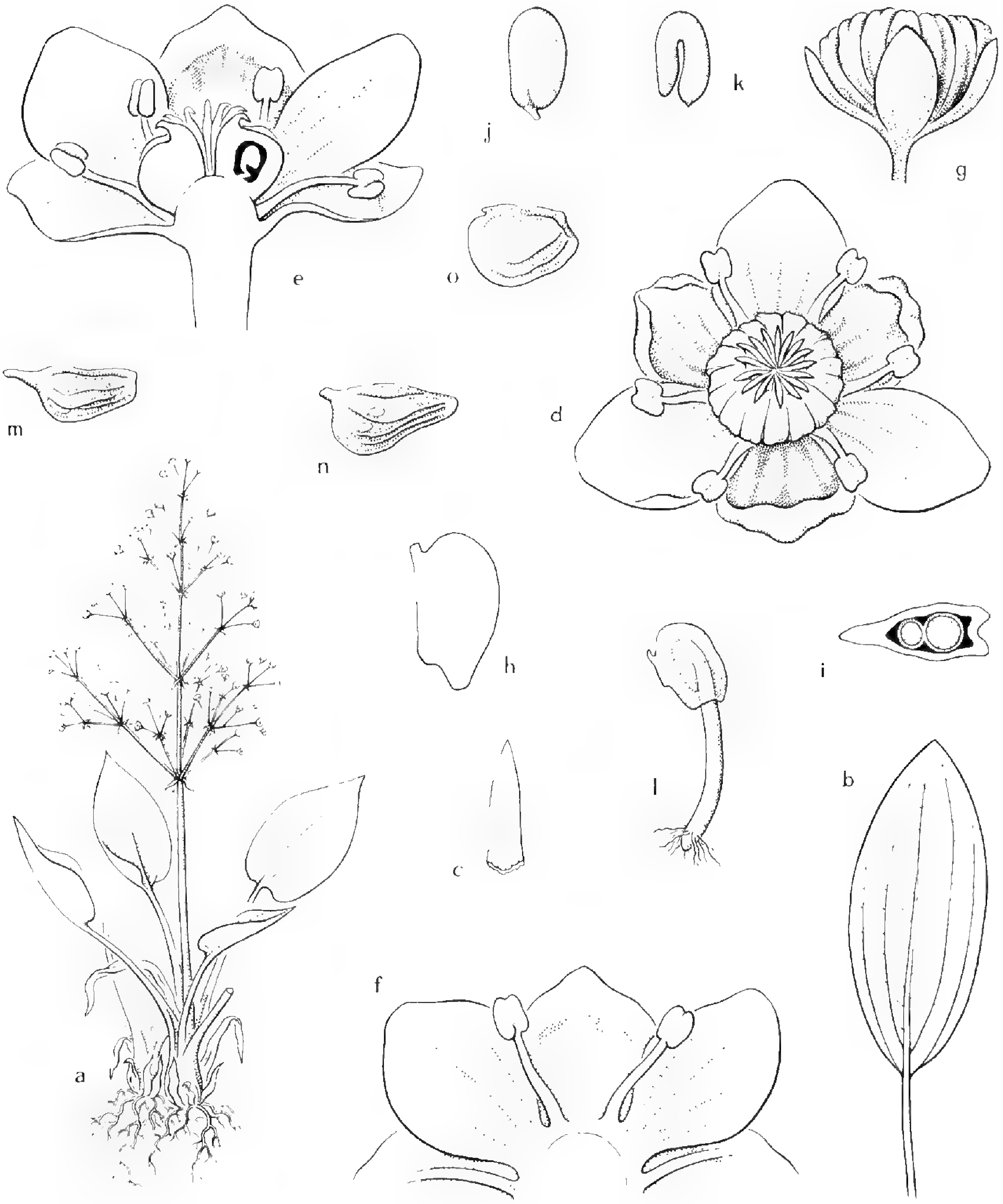

FIGURE 1. **Alisma** and **Echinodorus.** a–l, *A. subcordatum:* a, small plant with fruits, note base of second plant of axillary origin, × ¼; b, leaf blade, × ¾; c, bract from lower whorl of main axis of scape, × 1; d, flower, showing separate carpels in a ring, × 10; e, flower in vertical section slightly off center, carpel opened to show the single ovule, × 15; f, stamens, petals, and sepals from above, × 12; g, cluster of achenes enclosed by persistent sepals, × 10; h, achene, remnant of style at upper left, × 10; i, diagrammatic transverse section of achene cut near the middle, adaxial edge at left, pericarp unshaded, the 2 arms of the bent embryo at center (stippled) surrounded by thin seed coat, endosperm absent, × 15; j, seed, showing embryo beneath thin seed coat, endosperm absent, × 10; k, embryo, × 10; l, seedling emerging from achene, ring of anchoring root hairs at base of hypocotyl, × 6. m–o, achenes of *Echinodorus:* m, *E. Berteroi,* with pointed resin gland near apex, × 6; n, *E. cordifolius,* resin glands on side, × 6; o, *E. tenellus* var. *parvulus,* without resin glands, × 12.

lateral nerves usually originating from the base of the blade (sometimes from the midvein), extending to the apex or margin, interconnected by usually parallel and conspicuous veinlets (in some narrow leaves the veinlets arising pinnately from the midvein and extending to or nearly to the margin, or veinlets sometimes inconspicuous or absent). Scapes single or clustered, erect to prostrate, generally longer than the leaves, racemose, paniculate, or umbelliform, bearing at the nodes (pseudo-)whorls of sometimes basally connate, subulate to ovate [or oval] bracts, these subtending a variable number of pedicels and/or branches, often enclosing a cluster of smaller inner scales. Flowers perfect. Sepals with conspicuous longitudinal nerves, usually concave. Petals white or sometimes pink [rarely yellow], longer than the sepals, in our species rounded or emarginate at the apex; nectaries adaxial on the bases of petals and on carpels. Stamens (6–)9–30 [or more], with basifixed or versatile, latrorsely dehiscing anthers; pollen grains usually more or less spheroidal, with circular or irregularly shaped, granular pores, exine granular to spinulose (grains ovate to reniform with the exine reticulate in *E. Berteroi* fide Argue, 1976). Carpels numerous and free on a usually convex receptacle, variably elongate, each with an apical or lateral style. Fruit a usually spinose, aggregate head of beaked (beak small or absent in *E. tenellus* var. *parvulus*), ribbed [ribs rarely absent], compressed, elongate achenes, elliptic or widest above the middle, often slightly curved or roughly D-shaped, usually with 1 or more yellowish (dry) glands (absent in *E. tenellus*). Seed with a smooth or spotted integument. (Including *Helianthium* (Engelm. ex. J. D. Hooker) J. G. Smith in Britton, Manual, ed. 2. 54. 1905. Type species: *H. tenellum* (Martius) Britton = *E. tenellus* (Martius) Buch.) LECTOTYPE SPECIES: *Alisma rostratum* Nutt. = *Echinodorus Berteroi* (Sprengel) Fassett; see J. K. Small, N. Am. Fl. **17:** 46. 1909. (Name probably from Greek, *echinos,* hedgehog, and *doros,* a leather bag, in reference to the spinose achenes.) — BURHEADS.

Nearly 50 species in two subgenera and 13 sections distributed from the northern United States to Patagonia. Inasmuch as most of the species are from Central and South America and are known from meager collections (many by only one, and some only from cultivated plants), the genus as a whole remains poorly known. Over half of the species have been described within the last three decades, and more will surely be discovered with continued exploration in the neotropics. Hence generalizations about *Echinodorus*—especially those made before the efforts of Fassett and Rataj—still rest upon a superficial sampling. Three species of three sections from the two subgenera are indigenous to the United States, all of them occurring in the Southeast.

Subgenus HELIANTHIUM (Engelm. ex J. D. Hooker) Fassett (carpels 20 or fewer in a loose head, anthers basifixed) is represented by *Echinodorus tenellus* (Martius) Buch. (*Alisma tenellum* Martius, *E. parvulus* Engelm., *Helianthium parvulum* (Engelm.) Small). This member of sect. TENELLI Fassett (leaf blades linear-lanceolate to elliptic, ribs of achenes not crested, inflorescences with one or few whorls) ranges from the northern United States to southern Brazil. Fassett recognized four varieties; Rataj (1975), only two (he reduced one to synonymy with var. *tenellus* and elevated the other to the rank of species, thereby eliminating most of the West Indies from the range of *E. tenellus*). The variety in our area, *E. tenellus* var. *parvulus* (Engelm.) Fassett, treated by some recent authors as a distinct species, grows in Cuba and Mexico, and sporadically in the area defined by Texas, Kansas, Michigan (see Voss), Massachusetts (possibly extirpated in this state), and Florida (not in the Appalachians). Reports from the northern shore of Lake Superior remain questionable (see Agassiz, Parry, Scoggan, Rosendahl & Butters). These small plants are distinguished from the other two species in the Southeast by having (6–)9 (vs. 12 or more) stamens, no pellucid lines in the leaves, umbelliform inflorescences (vs. racemes or panicles), and achenes lacking glands and conspicuous beaks, and by their pseudostoloniferous habit (because of which this species sometimes forms mats).

Subgenus ECHINODORUS (carpels many in a dense head, anthers versatile) is represented in our area by two species from two sections. The sole species of sect. ECHINODORUS (sect. *Berteroii* Rataj) (strongly heterophyllous, stamens (9–)12, achenes rostrate, these with one gland or none), *Echinodorus Berteroi* (Sprengel) Fassett (*Alisma Berteroi* Sprengel, *A. rostratum* Nutt., *E. rostratus* (Nutt.) Engelm.), has often been confused with or included in our other species, *E. cordifolius* (L.) Griseb. (Hence "*E. cordifolius*" in literature before clarification by Fernald and Fassett should be interpreted with care.) *Echinodorus Berteroi* var. *Berteroi* (as circumscribed by Rataj) ($2n = 22$?; see Heiser & Whitaker) is distributed along the southern edge of the United States from mid-California to Georgia, and southward to southern Mexico; in much of the drainage of the Mississippi River in the area defined by Ohio, South Dakota, Oklahoma, and Arkansas; and throughout the West Indies. (See Fassett for discussion of doubtful reports that would broaden the range.) A disjunct variety (var. *patagonicus* Rataj) grows only in Argentina. *Echinodorus Berteroi* var. *lanceolatus* (Engelm.) Fassett (*E. cordifolius* var. *lanceolatus* Mack. & Bush) was found in Rataj's (1975) experiments to differ from var. *Berteroi* merely as a result of environment and was accordingly reduced to synonymy. This highly variable species produces at least three distinct forms of leaves and sometimes occurs as dwarf individuals only a fraction of the usual size.

Echinodorus Berteroi differs from *E. cordifolius* by having upright, often compound inflorescences; sepals with smooth (vs. papillose) abaxial nerves; glands (when present) extending farther toward the apex of the achene; and usually 12 (vs. over 20) stamens.

One of eight species of sect. CORDIFOLII Rataj (stamens 24–30, leaves with nonreticulate pellucid lines or spots), *Echinodorus cordifolius* (*A. cordifolia* L., *S. radicans* Nutt., *E. radicans* (Nutt.) Engelm.), $2n = 22$, is distributed along the Coastal Plain from southern Texas (and according to some reports in Mexico) to the vicinity of Washington, D. C., and in the drainage of the Mississippi River to mid-Tennessee in the east, extending westward to Kansas and Oklahoma and ranging north to central Illinois. Rataj (1975) reported this species in Venezuela. *Echinodorus cordifolius* differs conspicuously from the other two species in having young plantlets mixed with flowers at the nodes on arching or procumbent inflorescences. (Note, however, that De Wit reported that *E. Berteroi* under cultivation in deep water also forms plantlets on the inflorescence.)

Plantlets arise from vegetative buds on upright and horizontal inflorescences in several species of subg. ECHINODORUS, where such buds terminate lateral, bostrycoid, flower-bearing complexes and sometimes also occur singly in axils of bracts. In *Echinodorus tenellus, E. quadricostatus* Fassett emend. Rataj, and probably other species of subg. HELIANTHIUM, modified prostrate inflorescences on submersed individuals form only plantlets, never flower buds. These indeterminate, runnerlike pseudostolons resemble typical alismataceous inflorescences in bearing pseudowhorls of scale leaves at the nodes; on the pseudostolons the only other structure at each node is a single vegetative bud (Charlton, 1968, 1973).

Richard published the name *Echinodorus* in 1815 accompanied only by the scarcely informative "alismae polyandrae" long before Engelmann's generic description in the first edition of Gray's *Manual.* Buchenau (1868) listed 15 specific names and discussed the application of some of them. Micheli monographed *Echinodorus* in 1881 and included 17 species, about half of which have since been removed to other genera or have otherwise undergone changes in name. Buchenau contributed comments the following year, and a revision including 20 species in 1903. Fassett's treatment of the species in North America and the American tropics contains useful explanations of decisions concerning taxonomy and nomenclature. In a revision of the entire genus that followed preliminary papers, Rataj (1975; see also 1970, 1973, 1974, 1978), agreeing with Pichon and apparently with Fassett, diverged from Buchenau and Micheli by excluding all species in the Old World. Rataj's infrageneric classification corresponds closely to Fassett's, except that several species were added to both subgenera and subg. ECHINODORUS was subdivided into 11 sections.

Echinodorus and *Sagittaria,* both in Pichon's subtribe Sagittariinae, are more similar to each other than either is to *Alisma.* They both usually have achenes with glands or resin ducts on the faces, carpels crowded onto a dome-shaped receptacle, spherical pollen (vs. polyhedric in *Alisma*), and the diploid chromosome number of 22 (vs. multiples of $x = 7$ in *Alisma*; note, however, that the chromosome number is established for only one species of *Echinodorus*). *Echinodorus* differs from *Sagittaria* in having perfect (vs. usually imperfect or a combination of perfect and imperfect) flowers; usually plumper carpels and achenes; a stronger tendency toward bostrycoid complexes in the inflorescence (and thus more than three flowers per node); pollen grains with smaller spinules (Argue, 1976); one pair (vs. two or three pairs) of chromosomes with nearly median centromeres; and two (vs. no) pairs of chromosomes with satellites (see Baldwin & Speese; Beal, 1960). Although similar in appearance to the terminal pseudostolons produced by species of *Echinodorus,* stolons of *Sagittaria* are axillary branches.

Differences in the circumscription of *Echinodorus* complicate comparison of generalizations made about it by different authors. After the first appearance of the generic name but before the monographic works enumerated above, *Echinodorus* was usually included in *Alisma.* Baillon placed it under *Sagittaria.* Several species previously regarded as components of *Echinodorus* by one or more botanists have been the bases of other genera of Alismataceae. Among these are *Baldellia* (containing the often-mentioned *Echinodorus ranunculoides* (L.) Engelm.), *Ranalisma, Burnatia* M. Mich., *Rautanenia* Buch., *Albidella* Pichon, and *Helianthium.* Except for the last two, all are limited to the Old World. *Echinodorus* is compared with some of these genera in Argue (1976), Charlton (1973), Pichon, and Rataj (1975). Even as *Echinodorus* is circumscribed by modern authors, a troublesome heterogeneity has repeatedly been mentioned.

In 1974 Argue believed that palynological evidence substantiated the separation of *Baldellia* from *Echinodorus.* Similarly, Wodehouse thought that *Baldellia* (*Echinodorus*) *ranunculoides,* together with "*E. cordifolius*" (probably *E. Berteroi*), comprised a palynological type apart from five other species of *Echinodorus.* In a later survey involving 20 species of *Echinodorus,* Argue (1976) found that evidence from palynology "might ultimately provide some clues for its dismemberment" and assigned the pollen of *Baldellia* and *Echinodorus* to different morphological categories (acknowledging intermediacy), but he did not repeat his assertion of 1974. On the other hand, Charlton (1973) found *Baldellia ranunculoides* to show "strong similarities" to Fassett's sect. TENELLI (but not, he emphasized, subg. ECHINODORUS sensu Fassett) in having pseudostolons and a determinate, morphologically similar inflorescence. *Baldellia* differs from *Echinodorus* in its 6 (vs. usually more) stamens and tends to have more terminal styles.

Although *Ranalisma* likewise resembles species of *Echinodorus* in producing pseudostolons, those of *Ranalisma* (*humile*) differ in being sympodial (vs. monopodial) and in having bracts in pairs as opposed to pseudowhorls of three (Charlton, 1968, 1973; Charlton & Ahmed, 1973b). That the aerial inflorescences of *Ranalisma* are sympodial further separates *Ranalisma* from *Echinodorus* and from the Alismataceae in general (Charlton, 1968, 1973; Charlton & Ahmed, 1973b). Charlton & Ahmed (1973a, b) concluded that the sum of evidence from floral and vegetative structures indicates an isolated position for *Ranalisma* within the Alismataceae (*cf.* Gagnepain).

Development of secretory canals, a familial characteristic, reaches an extreme in leaves of species of *Echinodorus.* Sometimes branched, the canals may accompany veins or be free in the mesophyll. Appearing as translucent lines or spots or as a reticulum, these pellucid markings are helpful in recognizing the genus, and they vary sufficiently in shape, size, and distribution to serve as taxonomic characters for species. Elaboration on their structure and distribution can be found in Meyer's (1932) anatomical survey of leaves from several species.

All three species of *Echinodorus* in the Southeastern United States grow in permanently or periodically wet mud or sandy soil, usually in (or on the shores of) streams, ponds, temporary pools, ditches, marshes, and swamps. *Echinodorus Berteroi* tolerates "almost dry places" as well as brackish water according to Rataj (1975). Rand noted that *E. tenellus* seemed sometimes to bloom in Massachusetts while completely underwater.

Rataj (1975) indicated that hybridization occurs among several of the extraregional species and also noted alleged hybrids between *Echinodorus tenellus* var. *tenellus* and var. *parvulus.* Such hybrids were collected even in Texas and

Florida, states far from the geographic range he provided for var. *tenellus.* Certain collections suggested "introgression" between *E. Berteroi* and *E. cordifolius* to Fassett.

The intergeneric hybrid between *Echinodorus* (*Baldellia*) *ranunculoides* and *Alisma Plantago-aquatica* has been reported not entirely independently by Durand & Pittier, Glück (1913), Knobloch, and Wehrhahn. In a comprehensive comparison of supposed hybrids and parental species, Glück encountered numerous points of intermediacy, the most impressive in the anatomy of the fruit. Wehrhahn assigned the name *Alismodorus Muretii* to the plant he identified as resulting from the cross under consideration. However, after artificially pollinating over 100 flowers, Björkqvist (1968, see *Alisma*) failed to produce this hybrid and suggested alternative identifications for specimens and drawings considered by others to represent it.

Because of their attractive foliage (which is varied in color, texture, and shape), hardiness, ease of cultivation, and in some cases vegetative propagation from the inflorescence, species of *Echinodorus* are popular for cultivation in aquaria; at least 20 have been used this way, among them the three species native to the United States. Confusing disharmony between specific names applied by aquarists and those applied by taxonomists is partly alleviated in Rataj's revision. The plants are usually marketed as "Amazon swordplants" or under other names with "swordplant" a component, sometimes also as "cellophane plants" (e.g., *E. Berteroi,* with its membranaceous submersed leaves). (For information on *Echinodorus* in the aquarium see De Wit, Klee, Stodola, and Wendt.)

A phycomycete tentatively identified as *Aphanomyces euteiches* Drechsler caused severe loss of "*E. brevipedicellatus* Buch." (*E. amazonicus* Rataj?) at a nursery in Florida during 1970 and 1971. Four other species of *Echinodorus* appeared to be resistant to the disease (Ridings & Zettler).

In South America and the West Indies, species of *Echinodorus* are attributed with impressive medicinal benefits. Tea from the leaves, extract from underground parts, and other preparations have been used as an invigorating beverage, a diuretic, a laxative, and an astringent gargle. They have been used to clean and heal the skin, to "purify the blood," and to counter edema, various ailments of the kidneys and liver, and other afflictions (Corrêa, Peckolt, Penna, Roig y Mesa). As reported by Grosourdy, chopped roots (and, to a lesser extent, leaves) from *E. cordifolius* (*E. Berteroi*?) rubbed onto the skin cause blistering. "Tubers" of *E. grandiflorus* (Cham. & Schlecht.) M. Mich. are boiled and consumed by the Mataco Indians in Argentina (Steward). According to Torrey, Mohave Indians used "seeds" of *E. rostratus* (*E. Berteroi*?) as food. Brazilian species are used as a source of dye for textiles (Peckolt).

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3. **Sagittaria** Linnaeus, Sp. Pl. 993. 1753; Gen. Pl. ed. 5. 429. 1754.

Annual or (usually) perennial, often amphibious herbs. Usually glabrous (*S. latifolia* var. *pubescens* (Muhl.) J. G. Sm. and sometimes *S. guayanensis* HBK. pubescent on most organs, other species sometimes with pubescent filaments). Roots usually conspicuously septate. Most species producing one to many thin axillary stolons, these sometimes branching, sometimes forming a chain of

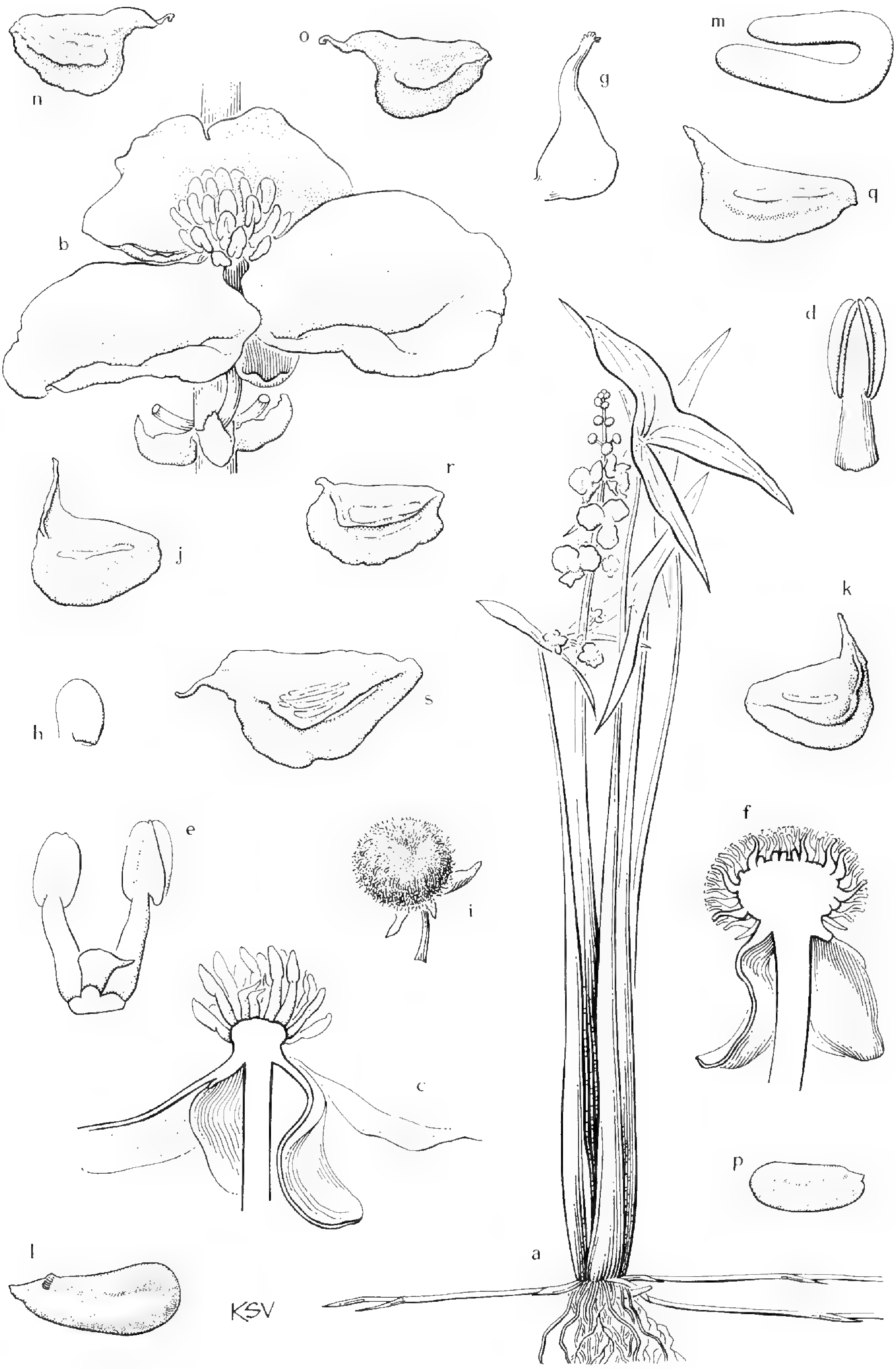

FIGURE 2. **Sagittaria.** a–m, *S. latifolia:* a, flowering plant with stolons, plant monoecious, the inflorescence with carpellate flowers below and staminate flowers above, × ¼; b, staminate flower, bracts and pedicels of 2 other flowers below, × 2; c, central

plantlets, the terminal bud often distal to an egg-shaped or subcylindrical storage organ comprised of 2 or more thickened internodes, this "tuber" sheathed in scale leaves, sometimes forming a plantlet or (in the year it was formed or after overwintering) the bud distal to the tuber growing into a new stolon, this sometimes very short and becoming vertical before terminating in a young plant. Plants usually with short upright stems sheathed (at least at the top) in leaf bases, some species with a horizontal rhizome bearing leaves along its length. Plants sometimes yielding milky sap when broken. Leaves highly variable in shape and size, submersed (then linear, flattened or terete to rarely sagittate-hastate, sometimes spongy), floating (then assuming almost the entire range of shapes, commonly elliptic or lanceolate), or growing out of water, then the blade linear to sagittate, usually acute to long-acuminate, sometimes rounded or obtuse at the apex, with a midrib and lateral nerves, these usually interconnected by more or less regular, parallel veinlets; petioles often spongy, especially at the broadened bases. Plants usually monoecious, with carpellate flowers toward the base of the scape, sometimes polygamous (then usually with staminate flowers distal to perfect flowers), sometimes dioecious. Scape(s) 1 to several per plant, erect or lax and floating, characteristically racemes, sometimes once branched at the basal node, on some small plants umbelliform or with only 1 flower, the main axis with up to 10(–18) nodes, each bearing a (pseudo-)whorl usually of 3 flowers subtended by usually basally connate, persistent or scarious, (often broadly) ovate to linear bracts. Flowers pedicellate (infrequently sessile). Petals white [rarely reddish or yellowish], sometimes with a dark spot at the base, larger than the sepals, usually with irregular margins. Nectaries on filaments, staminodes, and carpels, these sometimes modified. Staminate flowers with the sepals usually reflexed, sometimes with abortive carpels, stamens many in a dense cluster on the receptacle, the filaments tending to be dilated at or above the base, the anthers [linear or] narrowly to broadly elliptic-oblong, basifixed or dorsifixed near the base, dehiscence extrorse or latrorse. Pollen grains circular in outline, the pores often irregularly shaped, sexine usually markedly spinulose. Carpellate flowers sometimes with staminodes, the sepals appressed to reflexed, with numerous flattened carpels crowded on an expanded, rounded receptacle, the tapered styles shorter or longer than the ovaries, apical or adaxial; ovules anatropous. Perfect flowers appearing

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part of staminate flower in vertical section (note sterile carpels in center), × 3; d, abaxial side of stamen, anther dehiscing, × 6; e, adaxial side of 2 stamens and sterile carpel, × 6; f, vertical section of carpellate flower immediately after fall of petals, × 3; g, carpel from carpellate flower, × 12; h, anatropous ovule, × 25; i, fruiting "head," an aggregate of achenes, × 1; j, k, opposite sides of mature achene (note crest on side in "k," and resin duct on both sides), × 6; l, seed removed from achene, oriented as in achene in "k," × 12; m, embryo from soaked seed, oriented as in seed in "l," × 12. n–p, *S. australis:* n, o, opposite sides of achene, showing crest on both sides and lack of resin ducts, × 6; p, seed removed from achene, oriented as in achene in "o," × 12. q, *S. lancifolia:* achene with 1 resin duct, × 12. r, *S. graminea:* achene with 1 resin duct above crest and another below it, × 12. s, *S. Engelmanniana* subsp. *Engelmanniana:* achene with crest and several resin ducts, × 6.

like carpellate flowers but with stamens. Achenes usually strongly compressed, mostly obovate or dolabriform, the margins drawn more or less out into wings, the abaxial margin often broadest and often with an irregular edge (or both edges sometimes irregular), often with facial glands (resin ducts) and ribs, these frequently with irregular, even ornamented edges, the remnant of the style projecting laterally or apically from the apex or from the upper half of the adaxial edge. $x = 11$. (Including *Lophotocarpus* T. Durand.) LECTOTYPE SPECIES: *Sagittaria sagittifolia* L.; see J. K. Small, N. Am. Fl. **17:** 51. 1909. (Name from Latin *sagitta,* arrow, from the shape of some leaves, adopted by Linnaeus from earlier use.) — ARROWHEAD, WAPATO(O), DUCK-POTATO, SAGITTARIA.

Approximately 35 species, with subgenus SAGITTARIA distributed throughout the Northern Hemisphere, primarily in North America, from subarctic to subtropical and some tropical regions. The most widespread species in the New World, *S. latifolia* Willd., ranges from Canada to northern South America. *Sagittaria lancifolia* L. extends as far south as Brazil, perhaps beyond. Most species of subgenus LOPHOTOCARPUS are native to the New World between southeastern Canada and southern South America; *S. guayanensis* is pantropical. Disjunct populations of a number of species occur at great distances from their apparent natural ranges; for example, according to Aston, none of the four species in Australia is native. There are roughly 20 or more species in the United States, approximately three quarters of them in the Southeast.

Taxonomic confusion and disagreement make a definitive listing of species impossible. The enumerations below include the species within the range of the Generic Flora that were recognized by Bogin, plus others added in accordance with subsequent work. Bibliographic references and comments are provided to facilitate further efforts toward clarification and enumeration of the extensive synonymy. Only the most noteworthy synonyms are given.

Subgenus LOPHOTOCARPUS (T. Durand) Bogin (carpellate flowers with sepals appressed or spreading, pedicels recurved and thickened in fruit, flowers often perfect) is represented by *Sagittaria calycina* Engelm. (Beal, 1960), *S. guayanensis* (a weed in rice fields; Thieret, 1969), *S. montevidensis* Cham. & Schlecht. (adventive), and *S. subulata* (L.) Buch. (including or not *S. Kurziana* Glück and *S. stagnorum* Small).

Subgenus SAGITTARIA (carpellate flowers with sepals reflexed, pedicels typically ascending, or recurved but not thickened, flowers rarely perfect) is represented by *S. australis* (J. G. Sm.) Small (*S. longirostra* auct. non M. Mich.; see Beal, Hooper, & Rataj), *S. brevirostra* Mack. & Bush (Beal, Wooten, & Kaul), *S. Engelmanniana* J. G. Sm., *S. falcata* Pursh (Beal, 1960), *S. fasciculata* Beal (1960), *S. graminea* Michx., *S. lancifolia, S. latifolia* (*S. sagittifolia* L. var. *longirostra* M. Mich.), *S. papillosa* Buch., *S. platyphylla* (Engelm.) J. G. Sm. (Wooten, 1973b), *S. rigida* Pursh (probably in Tennessee), and *S. secundifolia* Kral. Whether or not *S. teres* S. Watson and especially *S. isoetiformis* J. G. Sm. are distinct from *S. graminea,* and whether *S. teres* ranges as far south as the Carolinas, are points of disagreement (see Beal, 1960, 1977, especially p. 60; Bogin; Godfrey & Adams; Godfrey & Wooten).

Probably only one of the three species originally assigned to *Sagittaria* by

Linnaeus, *S. sagittifolia,* belongs to the genus in its modern sense. Even though *S. trifolia* L. frequently appears in modern publications, the illustration of it that Linnaeus cited either is very inaccurate or represents a plant referable to some other genus (Bogin thought *Ranunculus*). The 13 species tentatively recognized by Micheli in 1881 reflect both a generally modern circumscription of *Sagittaria* and trouble with the long-standing question of its relationship with *Lophotocarpus.* Smith (1895, 1900), due in large part to discovery of new entities, recognized 23 species in North America alone. He differed from Micheli in not including any of the New World taxa within *S. sagittifolia,* a view upheld in all subsequent revisions. Buchenau (1903) included most of Smith's species among the 31 in *Das Pflanzenreich.* Stressing that examination of extensive materials revealed new intermediacy between previously recognized taxa, Bogin (1955) reduced the number of species to 20 (including those added by treating *Lophotocarpus* as a subgenus of *Sagittaria*). Rataj (1972a, b) counterbalanced the North American emphasis of the preceding studies by revising the species of the Old World, the West Indies, and Central and South America. With a small number of exceptions, his species and subgenera are congruent with those of Bogin.

The predominant problem concerning the delimitation of *Sagittaria* is its relationship with *Lophotocarpus* (*Lophiocarpus* Miq.), which appears as a subgenus of *Sagittaria* in recent revisions. *Lophotocarpus* has been thought to differ in being annual and polygamous (vs. without perfect flowers), in having hypogynous stamens (vs. stamens erroneously perceived as inserted above the receptacle in *Sagittaria*), and in having three (vs. two) pairs of chromosomes with nearly median centromeres (see Smith, 1895, 1900; Baldwin & Speese; and the other papers cited in this paragraph). Mason, who provided a taxonomic history of *Lophotocarpus,* argued that some distinctions have been inaccurately and unclearly described, that they are of insufficient character to allow unambiguous identifications, that conditions ascribed to one genus appear in the other, and that at least one species assigned to *Sagittaria* based on some of these characters is obviously closer to *Lophotocarpus* in other regards. Beal (1960) doubted the significance of the cytological difference (which was indeed based on only one species of *Lophotocarpus*). Evidence from floral vasculature and development and from palynology reinforce merging the genera (Argue, 1976; Kaul, 1967). After Pichon advocated synonymy, Bogin broadened the circumscription of *Lophotocarpus* and reduced it to a subgenus of *Sagittaria,* emphasizing the nature of the sepals and pedicels rather than the presence of perfect flowers. (Other distinguishing features of *Sagittaria* are presented in its comparison with the similar *Echinodorus* in the treatment of that genus.)

Bogin treated problematical complexes as species composed of infraspecific taxa. The largest, centered around *Sagittaria graminea,* has been studied by Wooten (1970; 1971a, b; 1973a, b). Drawing data from transplant experiments, experiments to assess environmental plasticity, chromatography, and analysis of edaphic factors, she established three varieties within this species, and with emphasis on edaphic considerations, observations in the field, and crossing studies, she recognized several additional species. (Note that *S. secundifolia* subsequently described by Kral also appears to be closely related to this assemblage.) Adams and Godfrey, employing observations on living populations and transplant experiments, did not think taxonomic recognition of any of the components of the *S. subulata* complex to be justified but advocated further studies of which Houk undertook one. (Later, Godfrey & Wooten recognized *S. stagnorum* and *S. Kurziana* as species distinct from *S. subulata.*) Crossing experiments, analysis of ecological parameters, and morphological observations contributed to the decision by Beal, Wooten, & Kaul to elevate Bogin's subspecies of the "*S. Engelmanniana* complex" to species.

Hybridization occurs, but to an as yet inadequately investigated degree. The plasticity of the plants and related taxonomic confusion make recognition of hybrids difficult. Crossing experiments have shown *Sagittaria graminea* to be interfertile with four other species (Wooten, 1973b), with other possibilities suspected (see Bogin). On the other hand, Beal *et al.* (1982) tried and failed to demonstrate interfertility among *S. australis, S. brevirostra, S. cuneata* Sheldon, *S. Engelmanniana,* and *S. latifolia.*

If a small number of possibly incorrect deviating reports are disregarded, *Sagittaria* appears to have the uniform chromosome number $2n = 22$ (Baldwin & Speese; Beal, 1960; Bloom; Bogin; Brown, 1946; Larsen; Löve & Löve; Oleson; Sharma). The only indication of polyploidy is the ca. 44 count by Bogin for *S. subulata* var. *gracillima* (S. Watson) J. G. Sm. Species of subg. SAGITTARIA have one long pair of chromosomes with nearly median centromeres, nine pairs of intermediate length with subterminal centromeres, and one short pair with submedian centromeres (Brown, 1946; Baldwin & Speese; but see Oleson for a somewhat different report).

Sagittarias grow in diverse aquatic habitats, commonly in shallow water or on wet banks in or bordering on streams, ponds, swamps, marshes, and ditches, sometimes in tidal areas, sometimes constantly submersed, and sometimes on sites that dry periodically. The degrees of submersion or drying tolerated by different species vary widely and are closely related to the diversity of their foliage.

The alismataceous propensities for submersed and juvenile leaves to be straplike phyllodia and for aerial leaves to have expanded blades reach extremes in *Sagittaria. Sagittaria* (*subulata* var.) *Kurziana* grows underwater and has linear leaves, these reportedly sometimes exceeding 3 m in length (said by one collector to be as long as 50 ft). At the other extreme (according to Bogin), *S. longiloba* Engelm. ex Torrey invariably forms emergent, sagittate leaves. Foliar variation in several species, among them *S. latifolia* and *S. sagittifolia,* spans most of the range in the genus. The relative roles of ecological and genetic control vary among the taxa, a matter in need of continued investigation. Within the *Sagittaria graminea* complex, Wooten (1970) demonstrated that differences in the forms of emergent leaves and phyllodia between seven populations (of three varieties and four ecotypes) are attributable more to genetic differences than to adjustment to depth of water. Generalization of Houk's similar conclusion from transplant experiments on "genecodemes" in the *S. subulata* complex must be tempered by observations made by Adams & Godfrey on populations of this complex. They showed great diversity in the forms of phyllodes at certain localities (in some populations ranging between linear and sagittate), with the shapes obviously related to the water regime and even changing from year to year. (Supplementary references dealing with foliar variation in *Sagittaria* are Arber, 1920; Glück, 1905; Glück & Kirchner; Hroudová; Schanderl; and Sculthorpe.)

Although usually described as monoecious, plants of subg. SAGITTARIA are at times entirely staminate or carpellate and often bear perfect flowers. In *Sagittaria latifolia,* staminate and carpellate flowers are of variable proportions in individual inflorescences, but of nearly equal overall frequency (Schaffner, 1924, 1929). After observing cultivated plants and wild populations, Wooten (1971b) concluded that whether the flowers are staminate or carpellate in this species was not affected by environmental fluctuations to which plants were subjected, and is therefore under genetic control; that monoecious plants are self fertile; that germination of achenes from dioecious plants is especially inhibited; that reproduction in dioecious populations (which sometimes form "unisexual" stands) may be mostly asexual; and that dioecious populations generally seem to be distributed along major rivers, which could convey their propagules. In *S. brevirostra,* Kaul (1979) found a ratio of more than three staminate flowers per carpellate flower to remain fairly constant over a decade in one lake, despite changes in environmental conditions.

In Europe and North America, floral visitation by an array of insects—mostly various flies and short-tongued bees—has been observed (Glück & Kirchner, Lovell, Robertson, Turner). In *Sagittaria subulata* completely submersed carpellate flowers possibly produce achenes (Adams & Godfrey).

Winged, sometimes ornamented achenes (as discussed under the family) are not the only disseminules: dispersal is also linked to asexual reproduction. In extensive, probably highly clonal stands large numbers of plants are sometimes connected by stolons (e.g., in the *S. subulata* complex). Flotation of tubers, rhizomes, and entire plants with buds at the base (described by Lohammar) surely brings about effective relocation. Moreover, as in species of *Echinodorus,* plantlets form at nodes within inflorescences of *S. subulata* (Adams & Godfrey; Buchenau, 1903).

Multiple proembryos in an embryo sac of *Sagittaria graminea* were interpreted by Johri (1936) probably to have resulted from fertilization of synergids by a second pollen tube.

A number of species of *Sagittaria* are cultivated as ornamentals. Doubled forms have been designated *S. japonica* Hort. (Porterfield, W. Smith). Several species (including *S. subulata*) producing attractive band-shaped leaves when submersed are grown in aquaria, sometimes under the name *S. natans* (see especially Wendt). Some serve as green manure (and as bothersome weeds) in rice fields, and as oxygenators in ponds where fish are raised.

Preparations involving sagittarias have been attributed with diverse medicinal benefits, primarily in eastern Asia, but also by North and South American Indians and others. Most commonly mentioned are applications to soothe and cleanse afflictions of the skin. In this connection it is noteworthy that Sharma and colleagues (1975b), during screening of Indian plants over a wide range of biological activities, observed antiinflammatory activity in an extract from *S. sagittifolia* from which they isolated a new diterpene, sagittariol. Conversely, contact with tubers or extracts from some species has caused dermatitis in humans (Mitchell & Rook, Morton).

Throughout most of its range *Sagittaria* is a source of food. Tubers of several species, produced abundantly toward the end of the growing season, are commonly compared to and prepared like potatoes. Baked, boiled, fried, ground into flour, or cooked in more elaborate fashion, the tubers are highly esteemed, but when raw they are acrid and likely to be toxic (Pammel, Stuart). *Sagittaria* is cultivated and the tubers marketed in eastern Asia, and it is sold among Chinese foods in the United States. American Indians, who acquired caches from the homes of muskrats and beavers, candied *Sagittaria* tubers with maple sugar or dried them for long-term storage. Not surprisingly, it has been suggested that human activity has historically played a role in the distribution of *Sagittaria.* (The tubers presumably were transported by ancient peoples, and the achenes from sagittarias growing as weeds probably contaminated rice.) The tubers remain popular among modern enthusiasts for edible wild plants. (Selected extra references concerned with *Sagittaria* as a source of remedies and nourishment are Fernald & Kinsey; Gibbons; Harrington; Peckolt; Perry; Porterfield; Smith, 1932, 1933; and Winton & Winton.)

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ARNOLD ARBORETUM
HARVARD UNIVERSITY
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

THE XYRIDACEAE IN THE SOUTHEASTERN UNITED STATES[1]

ROBERT KRAL

XYRIDACEAE C. A. Agardh, Aphor. Bot. 158. 1823, "Xyrideae," nom. cons.

(YELLOW-EYED GRASS FAMILY)

Annual or perennial, stemless to caulescent, usually rosulate, scapose terrestrial herbs of high-hydroperiod soils [rarely aquatic]. Roots mostly slender, diffuse-fibrous, with root hairs. Axis sympodial [or monopodial]. Leaves alternate, distichous or spiral, ligulate or eligulate, the bases broad, open-sheathing, frequently equitant and keeled, the blades laterally [to dorsiventrally] compressed, usually flattened, less often terete or ventrally sulcate, the indument usually of uniseriate-glandular, unbranched [to branched] trichomes [or absent]. Inflorescence(s) lateral [to terminal], the scapes 1 to few, arising from axils of scape sheaths [or inner leaves], naked [to short-bracteate], each bearing apically 1 [or more] imbricate-bracted spikes or heads [or a paniculate arrangement of same]. Flowers perfect, 1 to many, solitary and subsessile to pedicellate in the axils of chaffy, leathery, or scarious bracts. Perianth of 2 differentiated whorls. Sepals 3, the anterior (inner) one usually membranaceous and wrapped around the corolla, abscising as the flower opens, the other 2 subopposite, connivent [to basally connate], chaffy, boat shaped, usually keeled, clasping the mature capsule. Petals 3, equal [to unequal], distinct [to united and salverform], strongly clawed, the spreading blades broad, yellow to white [or blue]. Stamens usually 3, epipetalous. Staminodia 3, distinct, clawed as in petals and distally 2-armed, also moniliform-hairy or reduced [or absent]. Anthers 4-sporangiate, bilocular at anthesis, introrsely or laterally dehiscent, dehiscing longitudinally; pollen monosulcate or inaperturate. Gynoecium 3-carpellate, the ovary 1-locular [to incompletely 3-locular], the placentation marginal or parietal [basal, free-central, or axile]; style terminal, tubular, apically 3-branched; stigmas 3, truncated, glandular-hairy; ovules mostly numerous, anatropous, 2-integumented. Fruit

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The illustration was drawn by Karen S. Velmure from dissections by K. R. Robertson and C. E. Wood, Jr., of material collected by Norton G. Miller in North Carolina.

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capsular, mostly loculicidal; seeds usually numerous, mostly under 2 mm long, with strong longitudinal ridges and finer cross lines, translucent or farinose-opaque, the embryo small, situated at base of an abundant mealy endosperm. TYPE GENUS: *Xyris* L.

A pantropical family of four genera and nearly 300 species, most of them in *Xyris,* the only genus to range into the North Temperate Zone. The remaining genera (*Orectanthe* Maguire, *Achlyphila* Maguire & Wurdack, and *Abolboda* Humb. & Bonpl.) are small and are confined to northern South America.

The family is mainly distinguished by its combination of rosulate and scapose habit; it is also characterized by vessels with simple perforation plates in all vegetative organs; leaves with open sheaths and with narrow blades having parallel or uninerved venation; flowers solitary in axils of (usually) chaffy, imbricate bracts in conelike spicate or capitate inflorescences; perianth trimerous, heterochlamydeous, the sepals with the inside (anterior) member fugacious, membranaceous, and covering the rest of the flower in bud; androecium of 3 epipetalous stamens with anthers opening longitudinally and (usually) 3 staminodia; gynoecium tricarpellate; fruit capsular, typically loculicidal; and seeds small, with copious farinaceous endosperm.

Engler's placement of the Xyridaceae in the large and artificial order Farinosae together with 12 other families showing mealy endosperm and a usually compound superior ovary met with early opposition from many phylogenists. However, there seems to be general agreement in most recent studies that the family is closely related to the Rapateaceae, and both are placed either in the order Xyridales (Hutchinson, 1973) or, more popularly, in the Commelinales (Takhtajan, 1980; Cronquist, 1981; Thorne).

The four genera of Xyridaceae break into two groups (*Abolboda* and *Orectanthe* vs. *Achlyphila* and *Xyris*) on the basis of foliar and pollen characters. *Abolboda* and *Orectanthe* have spinose pollen, appendaged styles, and polystichous leaves with dorsiventral structure and commonly with a hypodermis of colorless cells under both surfaces. *Abolboda* (ca. 20 species) has an interior sepal that is reduced so that often only the lateral sepals are evident; a corolla that is regular and usually blue; staminodia that, if present, are simple and unbranched; and either styles that are apically three-branched or stigmas that are strongly hairy and trilobed. *Orectanthe* (*O. ptaritepuiana* (Steyerm.) Maguire and *O. sceptrum* (Oliver) Maguire) has three sepals, but the corolla is irregular and yellow, usually strongly curved outward with the interior lobe enfolding the other two lobes in bud; staminodia are lacking; and the style is simple, with the stigma subcapitate.

Achlyphila and *Xyris* have obviously or obscurely distichous leaves that are usually laterally compressed and lacking the colorless hypodermal layers. Their pollen lacks spines, their styles are unappendaged, and their corollas are regular. The monotypic *Achlyphila* (*A. disticha* Maguire & Wurdack) has an elongate, creeping, scaly rhizome from which arise erect, distichously leafy stems; it lacks staminodia and its styles are undivided. Members of *Xyris* are mostly short stemmed, have an outer sepal much different from the inner two, produce apically bipartite staminodia (in most), and have styles prominently three-branched above the middle. It is the only genus of the four that produces hairs on the leaves.

Tomlinson believes that, while *Abolboda* and *Orectanthe* are evidently closely related, *Achlyphila* may be a link between *Abolboda* and *Xyris,* thus making it more difficult to consider Abolbodaceae a distinct family, as did Nakai. Before the discovery of *Achlyphila,* Nakai's lead was temporarily followed by Takhtajan (1959).

The family is of little economic importance. Some species of *Xyris* are an important food for the wild turkey (*Meleagris gallopavo*) in the southeastern United States, some others are occasionally used as aquarium plants, and a few species with long scapes and conspicuous spikes are harvested for use in dried plant displays.

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1. **Xyris** Linnaeus, Sp. Pl. **1:** 41. 1753; Gen. Pl. ed. 5. 25. 1754.

Annual or perennial, short- [to prominently] caulescent, usually rosulate, scapose herbs with diffuse fibrous roots, usually perennating by lateral offshoot

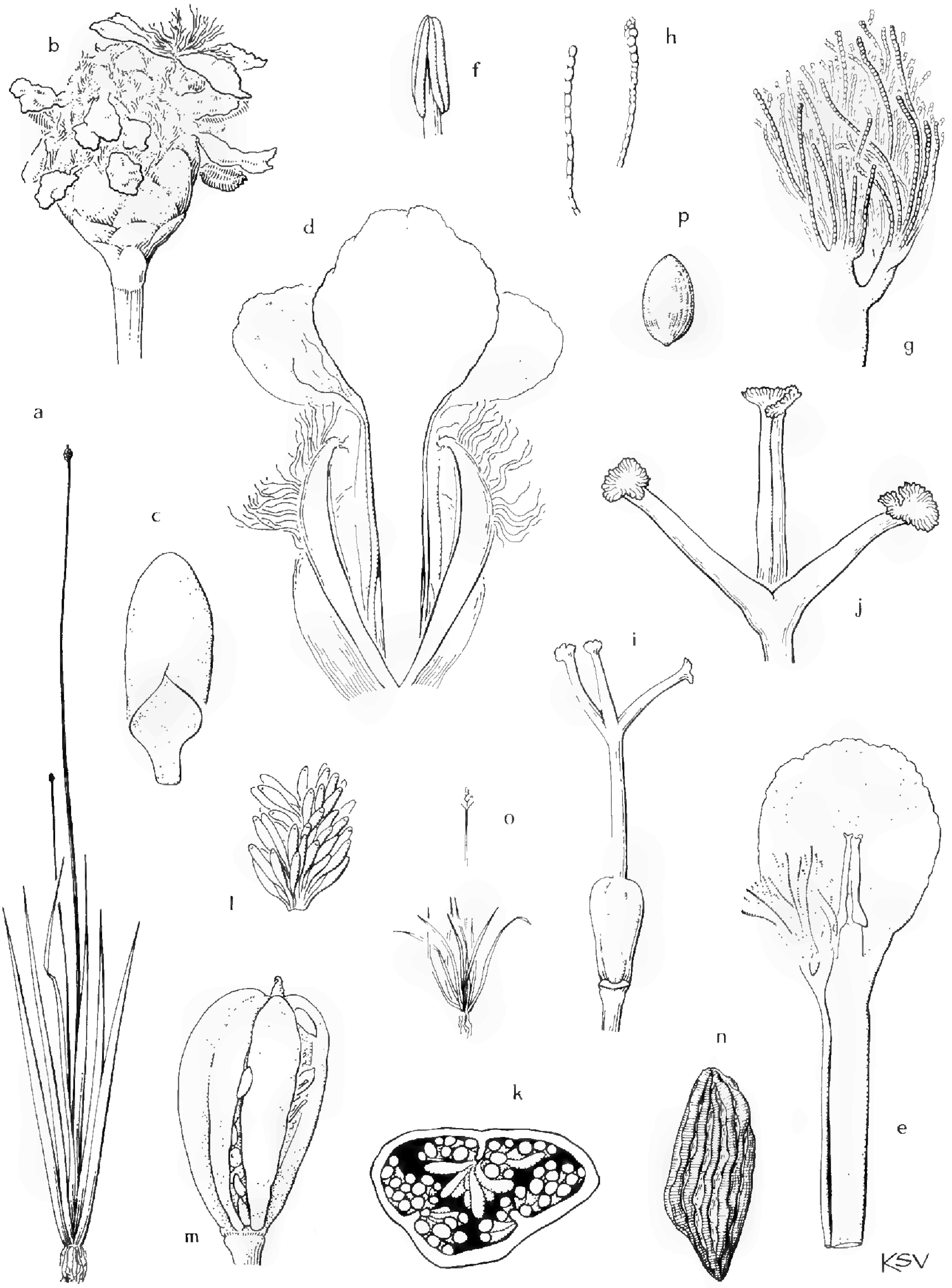

FIGURE 1. **Xyris.** a–n, *X. fimbriata:* a, habit, × ⅛; b, inflorescence, with 1 open flower and marcescent corollas of earlier flowers, × 2; c, inner (anterior) sepal, × 6; d, flower, from above, showing the 2 fimbriate lateral sepals and the subtending bract below (behind flower), × 5; e, petal with filament of fertile anther adnate to claw, and staminodium with free filament and much-branched tip, × 6; f, anther before dehiscence, × 6; g, tip of staminodium, × 12; h, moniliform trichomes of staminodium, × 25; i, gynoecium, × 5; j, tip of 3-parted style with stigmas, × 12; k, cross section of ovary, showing numerous orthotropous ovules on 3 parietal placentae, most ovules sectioned, × 20; l, adaxial side of 1 placenta with orthotropous ovules, × 12; m, dehiscing capsule, × 6; n, seed, × 40. o, p, *X. brevifolia:* o, habit, × ½; p, seed, × 40.

buds. Axis sympodial. Foliage externally smooth to variously papillose or rough [to pilose], often bearing uniseriate secretory trichomes on inner surfaces of leaf sheaths. Outer leaves often scalelike; principal leaves mainly linear, equitant, distichous, the sheathing bases open, usually strongly clasping and dilated distally, narrowing gradually or abruptly to junction with blade, there ligulate or eligulate, the sheath edges convergent to form one side, the midrib area the other, of a laterally flattened to terete, angulate or sulcate, usually linear, entire or scabrid [or ciliate] blade. Scapes single or few to a shoot, linear, terete to variously compressed, costate or ancipital, mostly overtopping leaves, each subtended by a sheath leaf that is closed and involute-tubular proximally, open and variously bladed [or bladeless] distally. Inflorescence a terminal, conelike head or spike of tightly to loosely spirally or distichously imbricate chaffy bracts, the lowest usually sterile and smaller than the fertile [less frequently, larger than the fertile and with cusps or blades overtopping the inflorescence], the fertile each with a subsessile axillary flower, sometimes the uppermost again barren. Sepals unequal, the 2 lateral opposing, connivent around the floral base, distinct (or variously connate), chaffy, boat shaped, variously keeled, equilateral or not, the anterior (inner) sepal scarious and enclosing the corolla in bud, fugacious. Petals free [to basally connate], subequal, long clawed, the blades usually broad, yellow [or orange], rarely white, spreading. Stamens equal, the short, fleshy filaments departing just above the petal claw, the anthers basifixed, 2-locular, the pollen monosulcate; staminodia 3, subequal, mostly 2-armed apically, the branches penicillate, with moniliform hairs [rarely glabrous or vestigial]. Ovary 1-locular [to imperfectly 3-locular]; ovules several to many, the placentae marginal or parietal [axile, basal, free-central]; style terminal, slender, tubular, strongly 3-branched above the middle, each branch terminating in a truncate, U-shaped or funnelform stigma fringed with glandular hairs. Capsule usually thin walled, 3-valved, dehiscing along 3 lines alternate with placentae. Seeds small, translucent or farinose, with copious mealy, starchy, proteinaceous endosperm, the embryo small, basal-lateral, the seed coat mostly longitudinally ribbed and cross lined. (*Kotsjiletti* Adanson, 1763; *Xuris* Adanson, 1763; *Xyroides* Thouars, 1806; *Jupica* Raf., 1836; *Ramotha* Raf., 1836; *Schizmaxon* Steudel, 1856.) TYPE SPECIES: *Xyris indica* L. (Name Greek, in reference to a plant with two-edged leaves, from *xyron,* a razor.) — YELLOW-EYED GRASS.

There are three sections: POMATOXYRIS Endl., with possibly 20 species, is characterized by axile placentation and is confined to Australia; XYRIS (sect. *Euxyris* Endl.), with ca. 100 species, is distinguished by marginal or parietal placentation and is predominantly pantropic and North American; NEMATOPUS Seub., by far the largest section and morphologically the most diverse, is characterized by basal or free-central placentation and centers in South America. No species are known from Europe, continental Asia, or (except for two species—one North American, one Asian—naturalized in Hawaii) the central or northern Pacific islands.

In the most recent treatment of North American *Xyris* (Kral, 1966), 19 species and three varieties were recorded for continental North America north of Mexico. One new species has been described since (Kral, 1978), bringing the total to 23 taxa, all of them indigenous and all confined in North America to the eastern United States and Canada. Most are limited to the Coastal Plain, with all but one either restricted to or occurring in the southeastern United States. Only three taxa grow in the wetlands of the Canadian Shield, and of these only *X. montana* Ries is confined to glaciated portions of the continent. Ten species are restricted to the southeastern United States, some as narrow endemics. Two are weeds of New World wetlands; seven center in the lower Coastal Plain terraces of Florida but also occur in the Caribbean (primarily western Cuba) and the pinelands or wet savannas of Belize, Honduras, Mexico, and Nicaragua. Fifteen additional species (five in sect. NEMATOPUS, ten in sect. XYRIS) are found in Mexico, Central America, and the Caribbean, with the majority endemic.

Gustaf O. A. Malme, European student of the Xyridaceae and in the early part of the century the recognized authority on *Xyris,* was the last to attempt formal subdivision of sect. XYRIS for North America (1937b). He delimited seven subsections, three monotypic and only one (*Mexicanae*) not represented north of Mexico. His artificial classification was based primarily upon characters of the lateral sepals (keels scabrid, ciliate, fimbriate, or villous, vs. keels entire), and secondarily on vegetative characters (e.g., leaf width, leaf length vs. scape-sheath length, degree of fleshiness of leaf-sheath bases). In contrast, the study of Brazilian xyrids by L. B. Smith and R. J. Downs (1968) pays far more attention to vegetative morphology—particularly foliar anatomy and inflorescence characters.

Relatively little has been done with the cytology of North American *Xyris* beyond some analyses of microsporocytes (Lewis, 1961; Kral, 1966). Twenty taxa have been so studied, and in all the counts have consistently been $n = 9$. A few root-tip studies (Kral, not yet published) have shown some genomal distinctness.

The flowers of *Xyris* are ephemeral, as is often the case in the Commelinales, with corollas normally not expanded for more than a few hours. Even in the southeastern United States, where several species may cohabit within a small area of wetlands, there may be wide differences between species or species complexes as to time of flowering within a 24-hour period. No nectaries have been found in any species in the genus, and few insects have been observed on the flowers. Only pollen-gathering bees (Bombidae, Andrenidae) have been noted, and to judge from the infrequency of even these visitors to *Xyris* flowers, it has to be concluded that North American xyrids are not obligately insect pollinated. Malme and others have speculated that the primary agent of pollination is wind, but there is considerable evidence (as yet to be tested) that much seed is set apomictically.

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Department of General Biology
Vanderbilt University
Nashville, Tennessee 37235

THE GENERA OF MENYANTHACEAE IN THE SOUTHEASTERN UNITED STATES[1]

CARROLL E. WOOD, JR.

MENYANTHACEAE Dumortier, Anal. Fam. Pl. 20, 25. 1829, "Menyanthideae."

Marsh, wetland, or aquatic perennial [or annual] herbs with alternate, simple or 3-foliolate, exstipulate leaves with sheathing petiole bases. Inflorescences various, monopodial or sympodial. Flowers regular (actinomorphic), perfect and often distylous, to imperfect. Calyx of 5 free or united sepals. Corolla sympetalous, 5-lobed, the lobes valvate or induplicate-valvate in bud, often with the margins and sometimes the inner surface fringed or bearded. Stamens 5, epipetalous, alternate with the corolla lobes, the anthers versatile, sagittate at base. Nectaries usually present at base of ovary. Gynoecium syncarpous, 2-carpellate, the calyx and corolla adnate to the lower part; style single, the stigma 2-lobed; ovary 1-locular, with numerous ovules on 2 (or 3) parietal placentae. Fruit a 2–4-valved capsule, or ± fleshy and irregularly dehiscent or indehiscent. Seeds numerous to few, usually smooth (or variously ornamented), with copious endosperm and a cylindrical embryo. (Tribe Menyantheae Griseb.) TYPE GENUS: *Menyanthes* L.

A small family of five genera and about 45 species: *Menyanthes* L., *Fauria* Franchet (*Nephrophyllidium* Gilg), and *Liparophyllum* J. D. Hooker, each with a single species; *Villarsia* Ventenat, with 12 species in Australia and one in South Africa; and *Nymphoides* Séguier, with about 30 species in Africa, Australia, tropical America, eastern North America, and Europe. *Menyanthes tri-*

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I am indebted to Dr. Norton Miller for his editorial and bibliographic help, and to Dr. Robert Ornduff, who has kindly read the manuscript and offered several suggestions and additional references. The illustration was prepared by the late Dorothy H. Marsh in 1957, long before Dr. Ornduff showed that *Nymphoides cordata* is dioecious. The living material came from Bateman's Pond in Concord, Massachusetts, where only the staminate plant occurs, and the other materials came from specimens in the Gray Herbarium from Florida (e, f, *Godfrey 55096 & Kral*), South Carolina (g, *Godfrey & Tryon 405*), and New York (h, *Muenscher 3541*).

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foliata L. is circumboreal in distribution. *Fauria Crista-galli* (Menzies ex Hooker) Makino is bicentric, with subsp. *Crista-galli,* $2n = 102$, in western North America (coastal Washington and British Columbia, northward to the Gulf of Alaska) and subsp. *japonica* (Franchet) Gillett, $2n = 68$, in eastern Asia (southern Kuril Islands, the Japanese islands of Hokkaido and Honshu, and southern Korea). *Liparophyllum Gunnii* J. D. Hooker is restricted to Tasmania and New Zealand.

Variously recognized as a tribe of the Gentianaceae (Grisebach, Bentham & Hooker), as a subfamily (Gilg, Rendle), or as a family (Cronquist, Hutchinson, Lindsay, Takhtajan, Thorne, Wagenitz), the Menyanthaceae differ from the Gentianaceae in their marsh or aquatic habitat; alternate, petiolate leaves; collateral vascular bundles; valvate or induplicate-valvate aestivation of the corolla lobes; fused lateral corolla traces and ± bilaterally symmetrical vascular plan in the flowers; tenuinucellar ovules with a single integument and integumentary tapetum; cellular endosperm development; and chemistry (loganin present, gentiopicrin and L-(+)-bornesitol absent). The Menyanthaceae are generally agreed to be related to the Gentianaceae but were placed in the Polemoniales by Cook and in the Solanales by Cronquist.

Nilsson has distinguished two pollen types in the family: the *Menyanthes* type (*Menyanthes, Fauria*), with "3-colporate, generally subprolate to prolate, striate to rugulose" grains; and the *Villarsia* type (*Villarsia, Nymphoides, Liparophyllum*), with "3-colporate, generally oblate to suboblate, parasyncolpate, striate, rugulose, spinulose, verrucose or ± smooth" grains. He found that pollen morphology supports an alliance of Menyanthaceae with Gentianaceae, *Menyanthes* and *Fauria* having pollen "similar to such genera as *Gentiana, Crawfurdia,* etc."

Heterostyly and associated self-incompatibility occur in *Fauria, Menyanthes, Nymphoides,* and *Villarsia. Liparophyllum* is monomorphic and self-compatible (Ornduff, 1982). Both homostylous self-compatible and heterostylous self-incompatible species occur in *Villarsia* (Ornduff, 1974), and dioecious species occur in *Nymphoides* (Ornduff, 1966). Gynodioecy has been recorded in *N. cristatum* (Vasudevan Nair). In heterostylous species pollen grains from short-styled flowers are larger than those from long-styled ones.

The family is of little economic consequence. *Menyanthes* has been used rarely in medicine. Several species of *Nymphoides* (especially *N. peltata*) are grown to a limited extent as ornamental, floating-leaved aquatics.

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KEY TO THE GENERA OF MENYANTHACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Marsh or aquatic herbs with simple or compound alternate leaves; corolla regular, sympetalous, the 5 stamens alternate with the 5 lobes; gynoecium syncarpous, 2-carpellate, adnate at the base to the perianth, the ovary 1-locular with 2 parietal placentae; fruit a dehiscent or indehiscent capsule.*

Leaves 3-foliate, emersed; palustrine herbs with a creeping rhizome; inflorescences racemose, emersed; corolla lobes valvate in bud; petals bearded on the inner surface; fruits borne above water, dehiscent, 2-valved. .... 1. *Menyanthes.*

Leaves simple, cordate to reniform, floating or submersed; aquatic herbs; inflorescences cymose, the flowers opening singly above water; corolla lobes induplicate-valvate in bud; petals not bearded on the inner surface; fruits ripening under water, indehiscent or opening irregularly. .... 2. *Nymphoides.*

1. **Menyanthes** Linnaeus, Sp. Pl. **1**: 145. 1753; Gen. Pl. ed. 5. 71. 1754.

Glabrous perennial aquatic herbs with creeping sympodial rhizomes bearing adventitious roots and a cluster of leaves at the apex; leaves and flowers emergent from water. Leaves alternate, ternate, petiolate, with large, membranaceous, sheathing bases. Inflorescences racemose on a leafless scape from the terminal bud of the rhizome. Flowers distylous (heterostylous, dimorphic), each subtended by a small bract. Calyx 5-lobed, synsepalous, the lobes partly recurved. Corolla deeply 5-lobed, pink outside, [pink to] white inside, the tube short, adnate to base of ovary, the lobes 3-veined, valvate in bud, the inside of lobes bearded with white fimbriae. Stamens at sinuses of lobes, the anthers basifixed, introrse. Style terminal, the stigma 2-lobed; ovary globular, the placentae parietal. Fruit a 2-valved loculicidal capsule, opening along lateral sutures, with numerous (ca. 20) seeds. Seeds light brown, shining, elliptical, slightly compressed, with abundant endosperm and a cylindrical embryo. LECTOTYPE SPECIES: *M. trifoliata* L.; typified by the transfer from *Menyanthes* to *Villarsia* of two of the three Linnaean species (Ventenat, Choix de Plantes, *pl. 9.* 1803); see also Britton & Brown, Illus. Fl. No. U. S. Canada. ed. 2. **3**: 17. 1913. (Name used by Theophrastus, from Greek *menyein,* disclosing, and *anthos,* flower; later applied to this genus with flowers expanding in succession in the raceme.) — BOG BEAN, BUCK BEAN.

The single species, *Menyanthes trifoliata,* $2n = 54$, is circumpolar in distribution in cold bogs, boggy meadows, fens, and shallow waters of pond margins, mainly between lat. 40°N and the Arctic Circle. It occurs in most of Europe but is rare in the Mediterranean region (Tutin), and it is distributed eastward to eastern Central Asia, Siberia, the Himalayas, Tibet, western China and Manchuria, Korea, Sakhalin, and Japan (Hokkaido, Honshu, and northern Kyushu) (Hara). In North America it is found from Greenland, Labrador, and

Newfoundland, west to Alaska, and south to the limit of the Wisconsinan glaciation, with scattered, often disjunct localities in the eastern United States in New Jersey, Delaware, and Pennsylvania, northern Virginia (Madison and Augusta counties), eastern West Virginia (Pocahontas County), northwesternmost North Carolina (Wautauga County), Ohio, Indiana, Illinois, Missouri (Reynolds County, in the southeastern Ozarks), and Nebraska. In the western United States it occurs mostly at higher altitudes south to Colorado, Montana, Wyoming, Nevada, California (in the Sierra Nevada), and southern Oregon.

Fernald segregated the eastern American representatives from the European plants as a weakly defined geographical variety (var. *minor* Raf.) on the basis of corolla size, color, and bearding of the upper surface of the lobes.

The species is distylous (or possibly monomorphic in some localities; see Avebury), but collectors seldom indicate whether both long- and short-styled forms are present in a given population. Long-styled plants of var. *trifoliata* have smaller pollen grains than short-styled ones (see Nilsson, Fossel & Vorwohl), but the situation is inconsistent in var. *minor* (Nilsson).

According to Guppy, seeds of *Menyanthes* float for two months. Ravn noted the buoyant seed coat. Ridley recorded that the seeds have been found in the excreta of reindeer, and in the crops of the European wild duck and the American mallard duck. Hochreutiner, who fed the seeds to three species of fish, found that nearly all germinated after passage (1–3 days) through the digestive tract.

On the basis of morphology, *Menyanthes* is presumably most closely related to *Fauria,* a relationship supported by pollen morphology.

The dried leaves of *Menyanthes* have been used as a substitute for hops in brewing. The very bitter juice has been used as a remedy for bowel trouble and dyspepsia; in large doses the effect is purgative and emetic. It has also been used as a tonic, an astringent, an antirheumatic, and a febrifuge.

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2. **Nymphoides** J. F. Séguier, Pl. Veron. (Stirp. Agro Veron. Reper.) **3:** 121. 1754.

Perennial rhizomatous herbs with floating, rounded to cordate leaves (superficially resembling miniature leaves of *Nymphaea* or *Nuphar*). Flowers borne in cymose, umbellike clusters (in our indigenous species at the summit of a slender, petiolelike internode with the petiole of the single floating leaf an apparent continuation of the stem), often with clusters of spurlike or "banana-like" tuberous adventitious roots. Plants [homostylous,] heterostylous (distylous), or dioecious (our indigenous species). Flowers emergent, the corollas white or yellow, delicate, 5-lobed, bearing 5 glandular, staminodelike tufts or fringes of trichomes near the base, 1 opposite each lobe; lobes induplicate-valvate in bud. In heterostylous species (e.g., *N. peltata*) flowers with styles either long and with well-developed 2-lobed stigmas and anthers borne below the level of the stigma on short filaments, or short and with smaller stigmas and anthers borne above the stigmatic level on long filaments; anthers dehiscing introrsely; pollen of long-styled flowers smaller than that of short-styled ones. In dioecious species gynoecium of staminate flowers lacking a style, the stigmas undeveloped, the ovules as large as those of carpellate flowers but nonfunc-

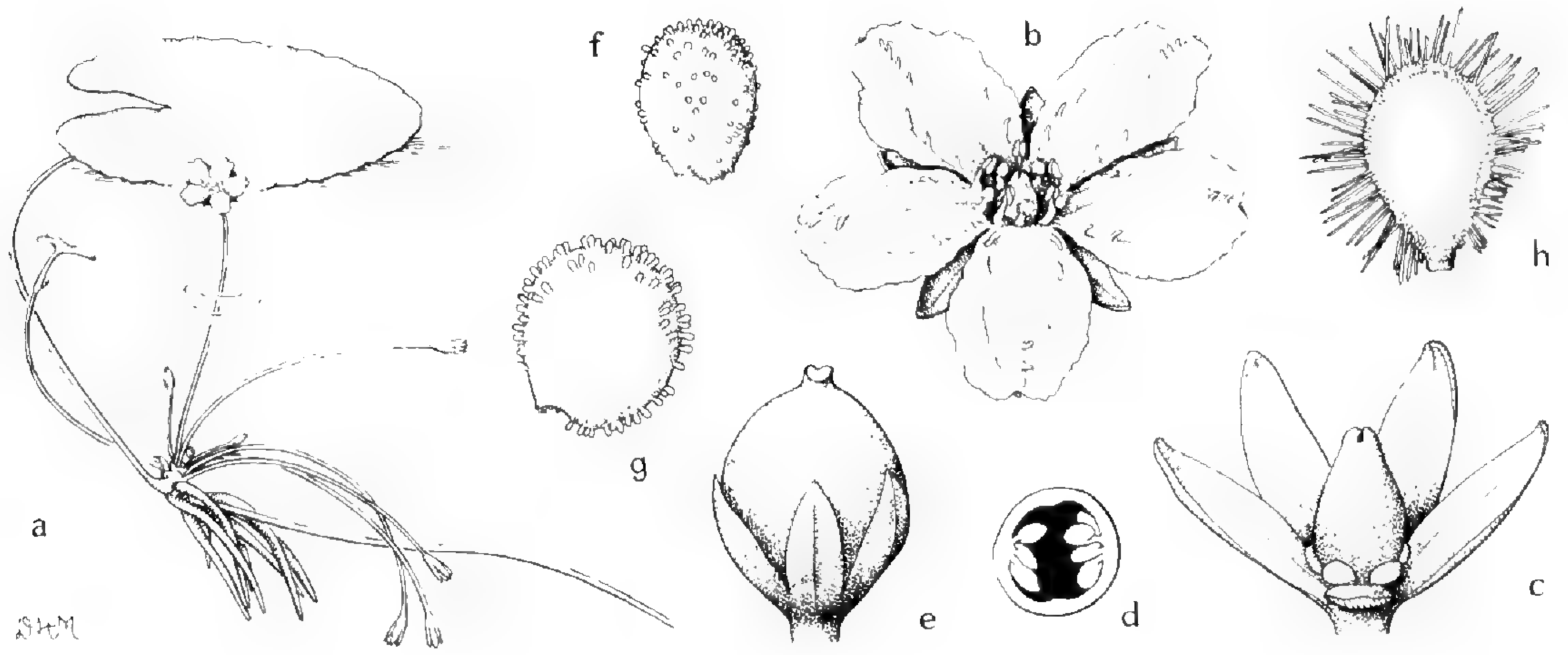

FIGURE 1. **Nymphoides.** a–f, *N. cordata:* a, floating leaf, inflorescence with spurlike adventitious roots, and small branch with unexpanded leaf and inflorescence, × ½; b, staminate flower, showing staminodiumlike appendages at base of petals and stamens alternating with petals, × 3; c, staminate flower, corolla removed to show sterile gynoecium and 4 of 5 nectar glands at base of ovary, × 6; d, cross section of ovary of staminate flower showing nonfunctional ovules, × 8; e, fruit, × 4; f, seed, × 10. g, *N. aquatica:* seed, × 10. h, *N. peltata:* seed, × 4.

tional; in carpellate flowers the style short, the stigmas well developed, fleshy. Five nectar glands present at base of ovary opposite base of corolla lobes. Fruits maturing under water, small, indehiscent or irregularly dehiscent with small, plump, nearly smooth to papillate seeds, or (in *N. peltata*) the capsules larger, resembling those of *Frasera,* the seeds larger, flat, their margins coarsely ciliate. (*Limnanthemum* S. G. Gmelin.) TYPE SPECIES: *Nymphoides aquis innatans* Tournefort = *N. peltata* (S. G. Gmelin) Kuntze. (Name from Greek, *nymphaia,* and *eidos,* resemblance, from the similarity of the leaves of *N. peltata* to those of the water lily, *Nymphaea.*) — FLOATING-HEART.

A genus of 30–35 species of floating-leaved aquatics, primarily of the tropics, best represented in the Old World (13 species in Africa and Madagascar, 12 species in Australia), with about five species in tropical America and two indigenous to eastern North America. *Nymphoides peltata,* the single Eurasian species, is often cultivated as an ornamental plant and is sporadically naturalized in the United States.

Nymphoides cordata (Ell.) Fern. (*N. lacunosa* sensu Fernald), $2n = 36$, is distributed in quiet "soft" (noncalcareous) waters from Louisiana and western Florida, northward on the Coastal Plain to New England, Nova Scotia, and Newfoundland, southwestern Quebec, and Ontario. It has thin, cordate-ovate floating leaves that are nearly smooth beneath and not densely dark pitted, capsules to 1.5 times the length of the calyx, and small seeds with a smooth to papillate surface. *Nymphoides aquatica* (J. F. Gmelin) Kuntze, banana floating-heart, $2n = 36$, a larger, coarser plant with ovate to reniform leaves with the lower surface usually thickened and densely dark pitted, the petiole and stem densely covered with dark glands, a capsule much larger than the calyx, and larger seeds with a tuberculate or papillate surface, is found on the Coastal

Plain from southern Florida west to eastern Texas, and north to Delaware and southern New Jersey. The corollas of *N. aquatica* are almost twice as large as those of *N. cordata*. However, corollas press so poorly (waxed paper or facial- or toilet-tissue should be used) that they are seldom adequately preserved in herbarium specimens of either these or other members of the genus.

Nymphoides peltata (*Limnanthemum peltatum* S. G. Gmelin, *L. Nymphoides* (L.) Hoffmans. & Link), yellow floating-heart, $2n = 54$, is indigenous to most of Europe north to Sweden and north-central Russia and is distributed eastward through the Caucasus to Iran, India, Taiwan, Mongolia, Manchuria, southern Siberia, Korea, and Japan. It is sporadically naturalized in the United States in New England, New York, New Jersey, Pennsylvania, Maryland, Ohio, Indiana, Illinois, Missouri, Arkansas, Mississippi, Louisiana, Oklahoma, Texas, Arizona, and Washington (see Stuckey). It is the best-studied species of the genus (see references). Sometimes forming dense stands in quiet waters, it overwinters by short-shoots that form new leaves and long-shoots in the spring. The flowering stems develop from a leaf axil of a long-shoot, and the flowers are produced sympodially in cymose, umbellike inflorescences. Each golden-yellow flower (ca. 3.5 cm across) lasts a single day, as in other species. The corolla absorbs ultraviolet light centrally and reflects it peripherally (Van der Velde & Van der Heijden), as do the yellow flowers of the Australian *N. geminata* (R. Br.) Kuntze (see Ornduff & Mosquin). Distyly is coupled with a weak self-incompatibility system. Van der Velde & Van der Heijden recorded 43 species of insects (mostly Apidae, Syrphidae, and Ephydridae) as visitors to the flowers in the Netherlands. Megagametophyte development is of the Polygonum type. The capsules mature under water one to two months after flowering, then burst open at the base. The flesh becomes soft and decays. The seeds float and are dispersed over the water surface by wind; they also adhere to water birds.

In both of our white-flowered indigenous species, the long, slender first internode of the inflorescence (see Goebel) is often misinterpreted as the long petiole of a floating leaf. Actually, each elongated stem bears a single floating leaf and is terminated by a flower; the cymose inflorescence develops sympodially as in *Nymphoides peltata* and is supported near the surface of the water by the floating leaf-blade (see FIGURE 1). In both species, fleshy spurlike (*N. cordata*) or somewhat banana-shaped (*N. aquatica*) adventitious roots are produced on either side of the inflorescence. These clusters function as overwintering vegetative reproductive structures. Both species are dioecious (Ornduff, 1966); collectors should note the occurrence of staminate and carpellate plants. The ultraviolet reflectance patterns have not been studied, but in the similarly white-flowered *N. indica* (L.) Kuntze the corolla absorbs ultraviolet light uniformly (Ornduff & Mosquin).

The genus includes diploids, tetraploids, and hexaploids ($2n = 18, 36, 54$). The American species studied thus far are tetraploids, and Ornduff (1969) found that the white-flowered tropical American tetraploids generally known as *Nymphoides Humboldtiana* (HBK.) Kuntze are conspecific with the Old World white-flowered diploid *N. indica*. Both homostylous self-compatibility and distylous self-incompatibility, as well as dioecism, occur in the genus. Ornduff

(1970) concluded that "dioecism has evolved at least two and perhaps three times in *Nymphoides*" and that it is "evident that tetraploidy has arisen independently in the genus more than once."

Nymphoides is closely related to *Villarsia* Vent., which has about 12 species in Australia and one in South Africa. In comparing the Australian members of the two genera, Aston (1969, 1973) pointed out that in *Nymphoides* the plants are true aquatics, the flowers are in nonpaniculate inflorescences, the pedicels bend downward after flowering, and the fruits ripen under water and are indehiscent or break up irregularly. In *Villarsia* the plants are mostly wetland herbs with erect paniculate (rarely condensed and capitate) inflorescences, the capsules are not carried under water for ripening, and the fruits are usually valvate capsules.

Nymphoides peltata, N. aquatica, and *N. indica* (including *N. Humboldtiana*) are cultivated in the United States to limited degrees for their attractive flowers and floating leaves. The somewhat bananalike adventitious roots from the inflorescences of *N. aquatica* are sold as an aquarium oddity, underwater banana plant.

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Also see family references, especially AGABABIAN & TUMANIAN; ANDREAS & COOPERRIDER; ARBER; ASTON; BAILEY, BAILEY *et al.*; COOK; GANDERS; GILLETT; GRISEBACH; GUÉGUEN; GUÉRIN; HARA; HEGI; KNOBLAUCH; LAWRENCE; LEBRETON & DANGY-CAYE; MUENSCHER; NETOLITZKY; NILSSON; ORNDUFF; PERROT; PROGEL; RICKETT; RORK; SCULTHORPE; STOLT; and TUTIN.

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Arnold Arboretum
22 Divinity Avenue
Cambridge, Massachusetts 02138

FLORAL STRUCTURE AND RELATIONSHIPS OF THE TRIMENIACEAE (LAURALES)

PETER K. ENDRESS AND F. B. SAMPSON

THE FAMILY Trimeniaceae is a small western Pacific group of the Laurales, formerly included in the Monimiaceae but separated as an independent family by Gibbs (1917) and, with a detailed discussion, by Money, Bailey, and Swamy (1950). It comprises two genera, *Trimenia* Seem. (three to seven species) and *Piptocalyx* Oliver (two species) (Perkins, 1925; Rodenburg, 1971; Smith, 1978), occurring in eastern Australia, Celebes, the Moluccas, New Guinea, New Britain, Bougainville, New Caledonia, Fiji, Samoa, and the Marquesas Islands (Perkins, 1925; Rodenburg, 1971; Van Balgooy, 1975).

This study, undertaken because the Trimeniaceae were poorly known and had not yet been studied comparatively, is an investigation of the floral structure of species of *Trimenia* and *Piptocalyx*. In addition, systematic relationships, both within the family and with other groups, are discussed.

MATERIAL AND METHODS

Floral material fixed in FAA was studied from the following species and collections:

Trimenia papuana Ridley
  Endress 4066 (cited in the text as *E 4066*), Aug. 1977, eastern Papua New Guinea (buds, flowers, fruits).
  Endress 4087, Aug. 1977, eastern Papua New Guinea (buds).
  Womersley s.n., Sept. 1970, eastern Papua New Guinea (buds, flowers).
Trimenia neocaledonica Baker f.
  McPherson 4044, Aug. 1981, New Caledonia (buds).
  Endress 6315, Sept. 1981, New Caledonia (buds, flowers).
Trimenia weinmanniifolia Seem.
  Siwatibau s.n., July 1971, Fiji (buds, young fruits).
Piptocalyx moorei Oliver
  Endress 4005, July 1977, Coffs Harbour, New South Wales, Australia (buds).
  Endress 4367, Sept. 1977, Coffs Harbour, New South Wales, Australia (buds, flowers).
  WELTU 13764 (*Sampson*), Aug. 1981, near Armidale, New South Wales, Australia (buds).

Plants of *Trimenia papuana, T. neocaledonica,* and *Piptocalyx moorei* were observed at anthesis in the field. Anatomical investigations were carried out

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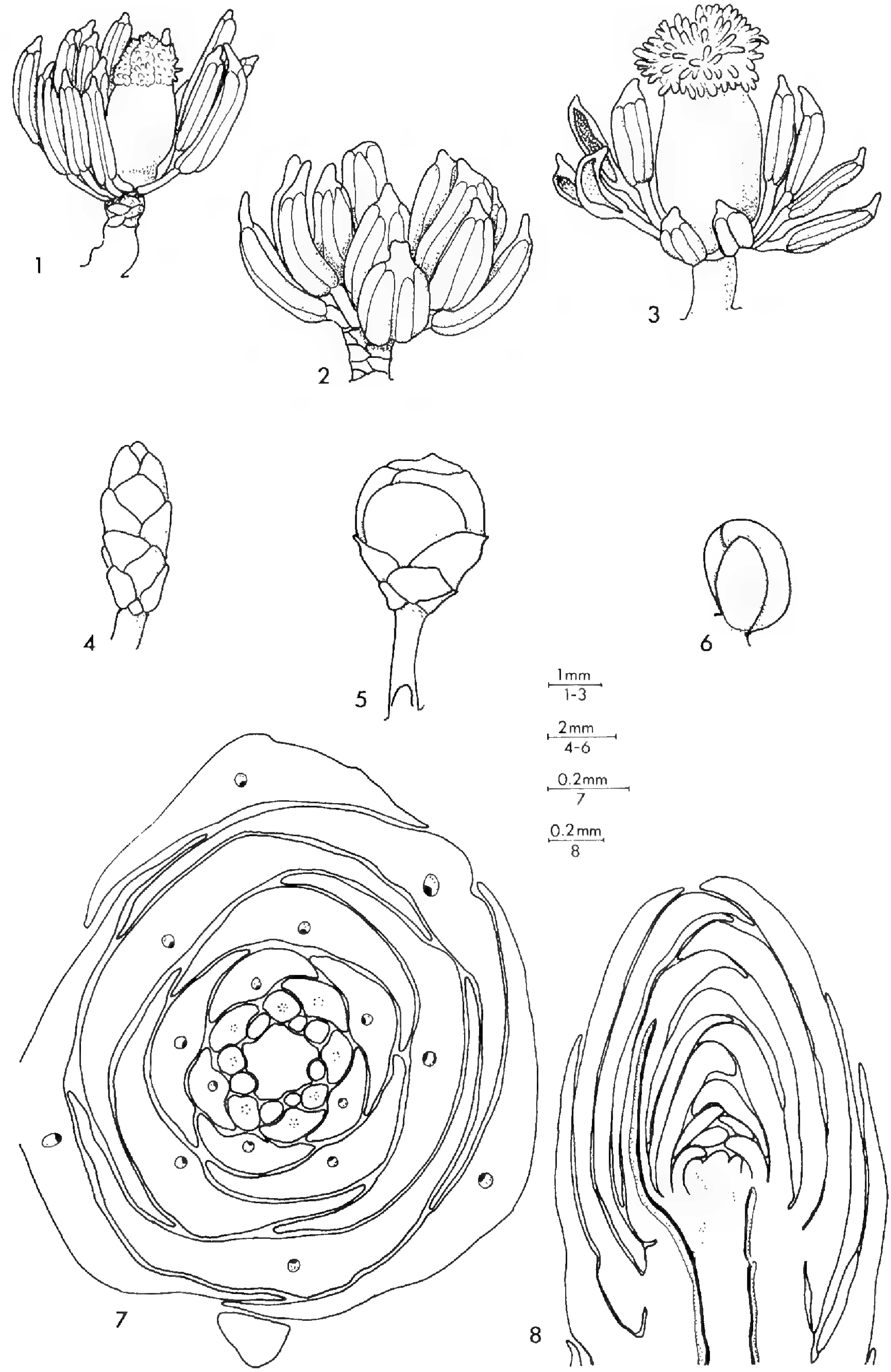

FIGURES 1–8. Flowers and buds. 1–3, flowers at anthesis: 1, *Trimenia papuana* (*E 4066*), hermaphroditic; 2, *T. neocaledonica* (*E 6315*), staminate; 3, *Piptocalyx moorei* (*E 4367*), hermaphroditic. 4–6, mature flower buds: 4, *T. papuana* (*E 4066*); 5, *T.*

with serial microtome sections stained with safranin and astra-blue or with Heidenhain's hematoxylin. In addition, pollen formation and development were studied by means of squashes made in iron aceto-carmine. Gynoecial structure and development were examined with the aid of a Philips 505 SEM at Victoria University of Wellington, New Zealand.

OBSERVATIONS

THE FLOWERS AT ANTHESIS

TRIMENIA PAPUANA. *Trimenia papuana* is a tree of tropical mountain forests. The paniculate inflorescences are produced in leaf axils and at the end of leafy shoots. They consist of many small, inconspicuous, scentless flowers. In our collections most flowers were hermaphroditic, but a few were staminate, with the gynoecium reduced or lacking. Whitish stamens with long, narrow anthers surround a normally single styleless carpel consisting of a green ovary and a terminal, tuftlike, white, dry stigma (FIGURE 1). The pollen is dry and is easily blown from open anthers. No nectar is produced. Flower visitors were not seen. These features give the impression that wind plays a major role in pollination. A peculiar feature is that before anthesis the outermost tepals fall off, and at full anthesis all the inconspicuous, brownish tepals have been shed.

OTHER SPECIES. The flowers of *Trimenia neocaledonica* (a tree) and *Piptocalyx moorei* (a vine), both occurring in subtropical rain forests, do not differ from those of *T. papuana* in the features described above (FIGURES 2, 3, 35).[1] Although the flowers have broader anthers and are thus slightly more showy, they too are probably predominantly wind pollinated. A difference is that in both of these species the inflorescences are fewer-flowered botryoids (racemelike panicles; for terminology see Troll, 1964). Both species are andromonoecious, with more male flowers than are present in *T. papuana.*

PHYLLOTAXY AND NUMBER OF FLORAL PARTS

TRIMENIA PAPUANA. Phyllotaxy was determined in four flowers (two from each of two collections). The mean divergence angles of all floral parts were 137.6° and 138.7° in specimen *E 4087,* and 138.2° and 138.4° in *W,* 1970. The average of all 136 divergence angles present in the four flowers was 138.2°. The most

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[1] Figures of inflorescences, flowers, or fruits of all species as proposed by Rodenburg (1971) have been published, some of them in remote places. Therefore, it seems reasonable to add the following iconography here: *Trimenia neocaledonica* (Rendle, Baker, & Moore, 1921; Morat & MacKee, 1977), *T. papuana* (Gilg & Schlechter, 1917; Brown, 1935; Kanehira & Hatusima, 1942; Money, Bailey, & Swamy, 1950; Smith, 1978), *T. weinmanniifolia* (Seemann, 1871; Perkins & Gilg, 1901; Hutchinson, 1973; Smith, 1978, 1981), *Piptocalyx moorei* (Maiden & Baker, 1895; Oliver, 1895; Perkins, 1911; Beadle, 1972), and *P. macrurus* (Gilg & Schlechter, 1917, 1923).

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neocaledonica (*M 4044*); 6, *P. moorei* (*W 13764*). 7, 8, *T. papuana* (*E 4087*), sections of flower bud at time of initiation of inner stamens: 7, transverse; 8, longitudinal (dotted areas, procambium, with phloem in differentiated vascular bundles; black areas, xylem).

regular values were obtained from flower buds in which the innermost floral parts had just been initiated.

The phyllotaxy of the flowers is spiral, with more or less constant divergence angles approaching the "limiting divergence" (137.5°) of the Fibonacci series (Figures 7, 41, 42). The constancy is also maintained at the transition from the perianth to the androecium and that from the androecium to the unicarpellate gynoecium (Figure 53). In terminal flowers the outermost "tepals" (ca. 6) are often arranged in decussate pairs before the spiral phyllotaxy starts, thus continuing the decussate phyllotaxy of the bracts on the inflorescence axis. We call them tepals because there is no abrupt change between these organs in phyllotaxy, shape, or internode length. In lateral flowers the first two phyllomes take the position of prophylls. They are situated transversely, with a somewhat larger angle to the anterior than to the posterior. It is also useful to call these organs tepals because they are not distinctive in shape or internode length from the following ones (tepals).

Thirty flowers (ten from each of three collections) revealed the following range in the number of floral parts: perianth (P), (13 to) 17 to 25 (to 28); androecium (A), 14 to 25; and gynoecium (G) (0 or) 1 (or 2). Thus, the range given by Rodenburg (1971) is extended by our collections. This result reemphasizes the wide range of variation in number of floral parts in flowers with a spiral phyllotaxy.

Because the stamens have a narrow base, they can be distinguished from tepals even at early stages in development, in spite of the unaltered phyllotaxy and similar marked plastochrons (Figures 7, 41). Toward the end of androecium initiation, the roundish floral apex decreases in size and becomes more or less five-angled in outline due to the effect of the adjoining stamens (Figure 53).

OTHER SPECIES. In *Trimenia weinmanniifolia* and *Piptocalyx moorei* the floral phyllotaxy is the same as in *T. papuana.* The flowers of these species are spirally arranged, with the mean divergence angle approaching 137.5°. Divergence angles were not measured in *T. neocaledonica* because young enough buds were not available, but the arrangement is clearly spiral. *Trimenia neocaledonica* differs from *T. papuana* and *P. moorei* in often having the first two (transverse) phyllomes at some distance from the flower at the base of the pedicel (Figures 4–6). (Such flowers were not included in the count of organ numbers.) Thus, the limits between "prophylls" and "tepals" are not clear-cut in this group.

The range in number of floral organs in the three species (from twenty flowers of each) is:

Trimenia weinmanniifolia (*S*, 1971)
P, 14 to 23 A, 7 to 12 G, 0 or 1

T. neocaledonica (*M 4044*)
P, 15 to 21 A, 11 to 15 G, 0 or 1

Piptocalyx moorei (*E 4005*, *W 13764*)
P, 2 to 11 A, 7 to 16 G, 0 or 1 (or 2)

PERIANTH

TRIMENIA PAPUANA. The 13 to 28 tepals gradually change in size and shape from the smaller, roundish or depressed-obovate outermost ones to the larger, obovate to spathulate inner ones (FIGURES 9, 33). The spathulate tepals form hoods over the androecium by virtue of their apically broadened and curved flanks (FIGURE 9, nos. 11–14). The outermost tepals have thick bases, with a basal extension resembling a hypopeltate bract on the dorsal side (FIGURES 8; 9, nos. 1–9; 39; 40; cf. Endress, 1975). Small-celled abscission tissue is differentiated at the base of each tepal (FIGURE 40). Abscission of a tepal starts adaxially. Toward the center of the flower the tepals become thinner, and marginal parts may be reduced to a single cell in thickness. All tepals have a single unbranched vein. The outer tepals bear uniseriate, tricellular hairs on the margins that are exposed in the bud. Each hair has an elongated apical cell. The inner tepals are glabrous.

OTHER SPECIES. In *Trimenia weinmanniifolia* the 14 to 23 tepals do not differ from those of *T. papuana* described above.

In *Trimenia neocaledonica* all 15 to 21 tepals are roundish. The outermost ones are much smaller than the inner. The basal extension is less marked than in *T. papuana*. The veins are unbranched in the outer tepals and laterally branched in the inner ones; the innermost tepal again has simplified vasculature (FIGURE 10). All tepals are glabrous.

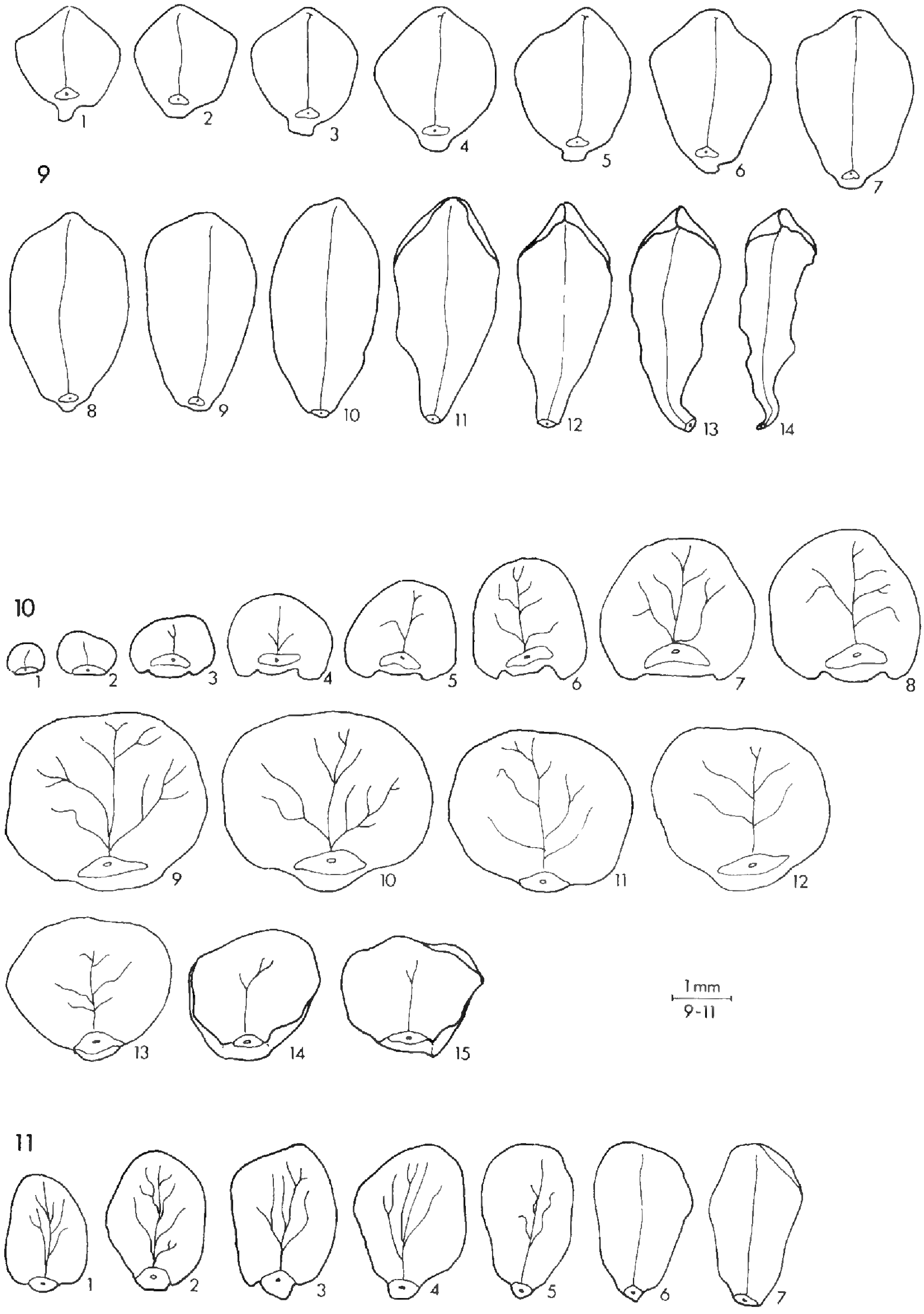
The 2 to 11 tepals of *Piptocalyx moorei* are ovate to obovate and lack a marked basal extension. The veins are branched in the outer tepals and simple in the inner ones (FIGURE 11). However, as in the other taxa, there is always only one trace to each tepal. The outer surface of the outer tepals is pilose where it has not been covered by other tepals or by the subtending bract in the young bud. The tricellular hairs resemble those of *Trimenia papuana*.

ANDROECIUM

In *Trimenia papuana* the 14 to 25 stamens are ca. 4 mm long and slender (FIGURES 13, 14, 34). The anther and the filament are equal in length. The mature anther is latrorsely dehiscent, opening by two lateral slits (FIGURE 17). It is capped by a short, linguiform connective apex. One collateral vascular bundle serves the stamen, ending in the connective apex in a group of short, tracheidlike cells. In a few flowers transitional forms between tepals and stamens have been seen; these were spathulate organs with a rudimentary pollen sac situated toward the base (FIGURE 12).

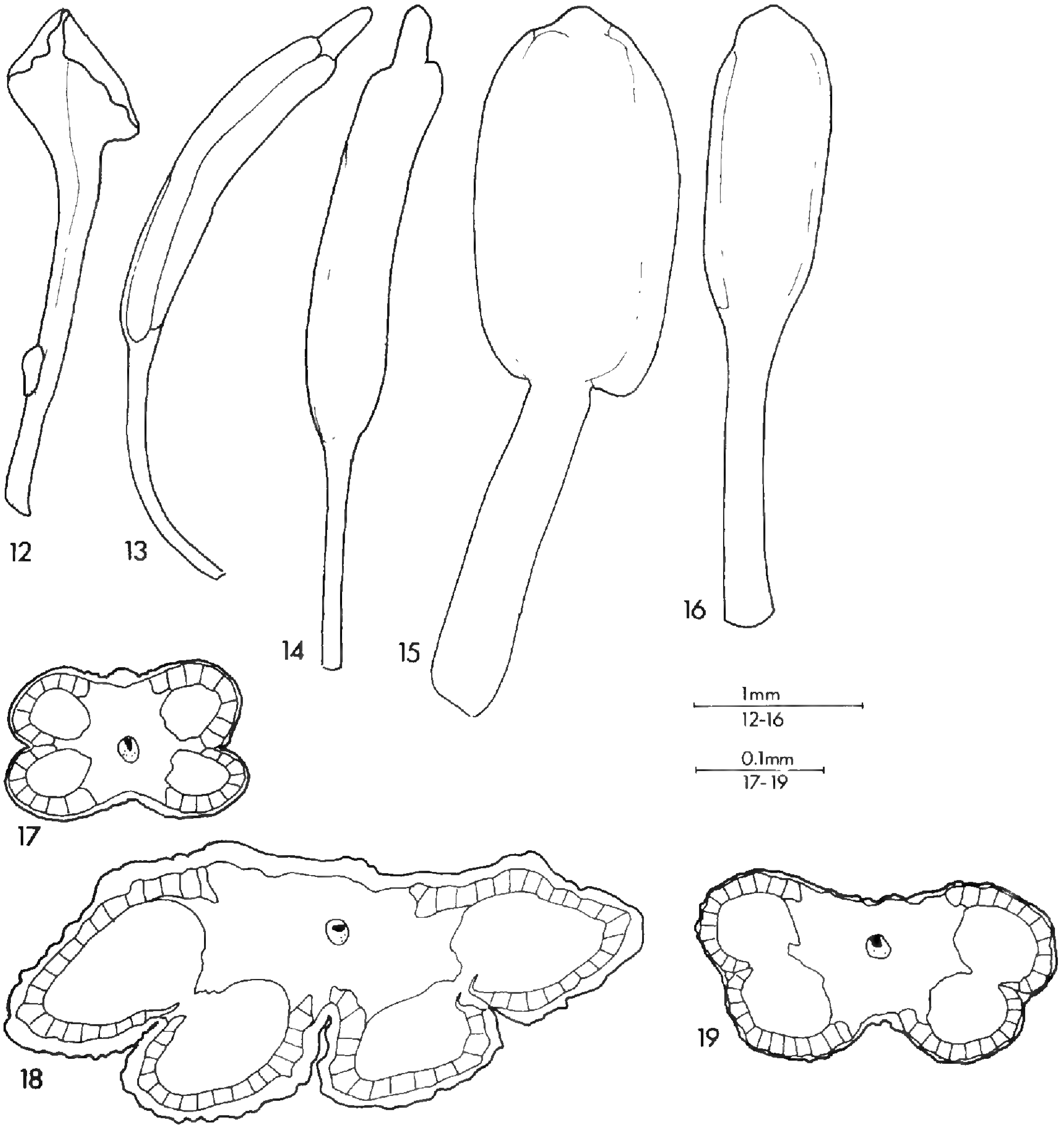
Although the 11 to 15 stamens of *Trimenia neocaledonica* and the 7 to 16 of *Piptocalyx moorei* are of about the same length as those of *T. papuana*, they have much broader filaments and broader, extrorsely dehiscent anthers (FIGURES 15, 16, 18, 19, 43). In all three species there is a considerable increase in filament length from the time tepals are detached to when pollen is shed.

The anthers are tetrasporangiate in all species. Both genera have microsporangia with large, persistent epidermal cells (smallest in *Trimenia papuana*, largest in *T. neocaledonica*) and an endothecium that develops the characteristic



FIGURES 9–11. Tepals of mature flower buds (each sequence from one bud), adaxial view: 9, *Trimenia papuana* (*E 4066*), outermost tepals not drawn; 10, *T. neocaledonica* (*E 6315*); 11, *Piptocalyx moorei* (*E 4367*).

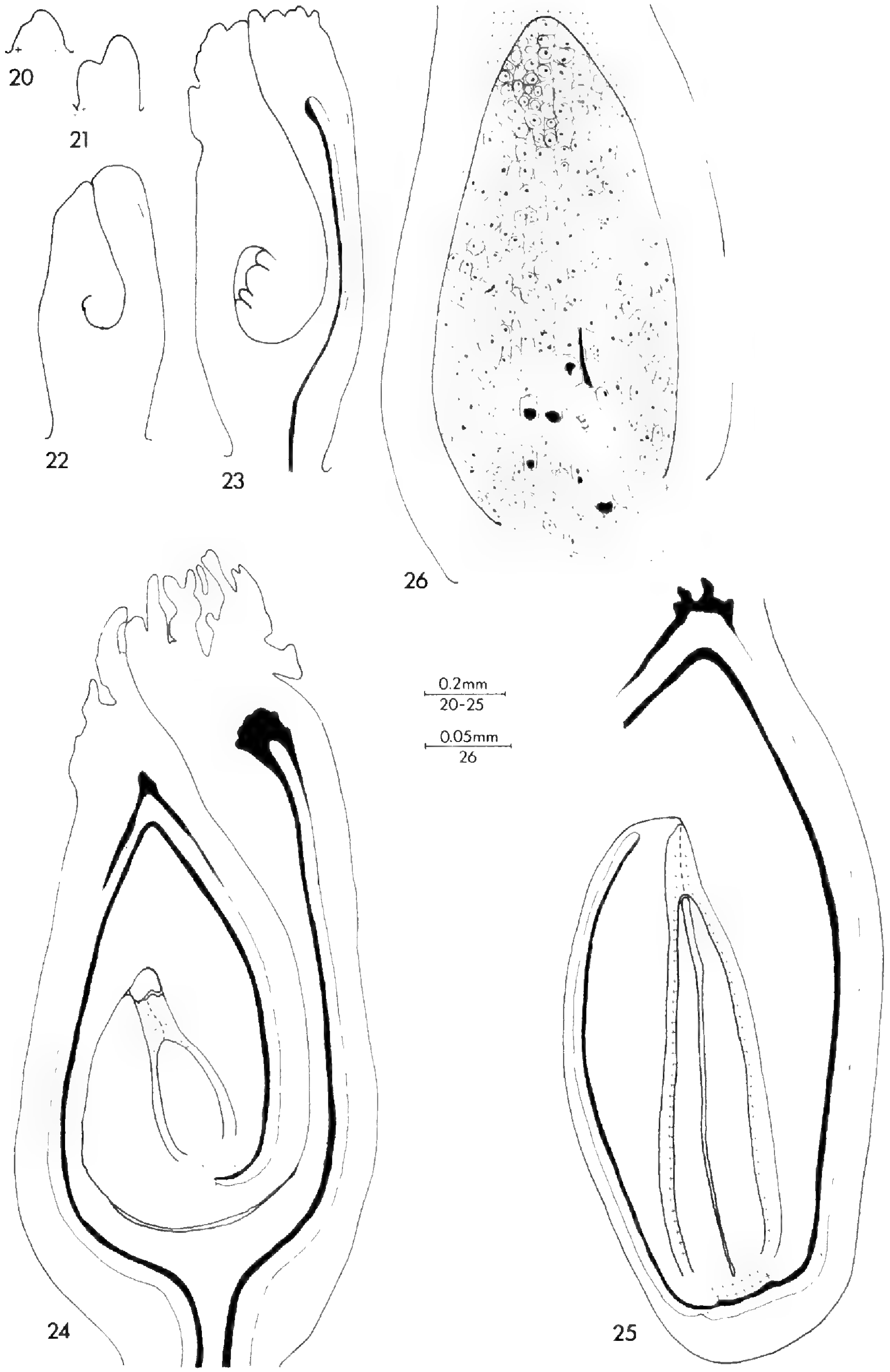
fibrous radial bars of thickening. The endothecium is restricted to the external part of each theca and is absent in the connective (FIGURE 43), which has a high tannin content. There is an irregularly one- or two-layered middle wall region that becomes crushed before anthesis. FIGURE 44 illustrates a stage in



FIGURES 12–19. Stamens. 12, *Trimenia papuana* (*E 4066*), innermost tepal with rudimentary pollen sac, adaxial view, from mature bud. 13, *T. papuana* (*E 4066*), stamen at anthesis, lateral view (right side = adaxial). 14–16, stamens at anthesis, abaxial view: 14, *T. papuana* (*E 4066*); 15, *T. neocaledonica* (*E 6315*); 16, *Piptocalyx moorei* (*E 4367*). 17–19, anthers shortly before dehiscence, transverse sections, adaxial side above, endothecium hatched: 17, *T. papuana* (*E 4066*); 18, *T. neocaledonica* (*E 6315*); 19, *P. moorei* (*E 4367*).

the development of the microsporangium of *Piptocalyx moorei* after the epidermis, endothecium, and middle wall layer have been differentiated. A single-layered tapetum encloses sporogenous tissue that is still undergoing cell division (not visible in the photograph).

The tapetum is glandular, and by the time pollen mother cells have reached the early stages in prophase I of meiosis, most tapetal cells are binucleate (*Trimenia papuana, Piptocalyx moorei*). Microsporogenesis was observed in *T. papuana*. Cytokinesis is of the successive type, with wall formation by a centrifugal cell plate occurring at the end of meiosis I and II (FIGURES 45, 46).



FIGURES 20–26. *Trimenia papuana,* carpel development, median longitudinal sections (left side = adaxial): 20, origin of ventral "cross zone" (*E 4087*); 21, chairlike stage (*W,* 1970); 22, early epidermal periclinal divisions in future stigmatic region (cell rows

The resulting tetrads are isobilateral, decussate, or intermediate between these types. In the limited material examined (several buds from a single collection), division stages were synchronized in each microsporangium throughout meiosis—an unusual feature. Although early stages in the division of pollen mother cells are normally synchronous due to linkage by cytoplasmic channels, exact synchroneity is usually subsequently lost when a callose wall forms around each meiocyte (Heslop-Harrison, 1966). Individual microspores within a tetrad are bilaterally symmetrical (FIGURE 47). Due to dissolution of callose wall material, microspores have a plano-convex shape for a time after they have separated; this reveals their orientation when they are in tetrads. Thus in FIGURE 48 the center of the curved edge of the microspore is at the distal pole. With maturation the pollen grains of *T. papuana* become more rounded, but they retain an ellipsoid (rather than spherical) shape. When pollen mitosis occurs, the generative cell is cut off so that it lies midway between the two more pointed ends of the grain. This is also the case in *T. neocaledonica* (FIGURE 49) and *P. moorei*. In these two species pollen is biaperturate, with the centers of the apertures located at the two more pointed ends of each grain. This is in contrast to *T. papuana,* which in our collections had inaperturate pollen (Sampson & Endress, in press). Polyforate pollen has been reported in some collections of this species (Walker, 1976) and in *T. weinmanniifolia* (Money, Bailey, & Swamy, 1950). Although our material of *T. neocaledonica* and *P. moorei* did not contain stages with pollen in tetrads, we assume (by analogy with *T. papuana*) that the more pointed ends of the grains are equatorially aligned and therefore that the pollen is disulculate (in the terminology of Walker, 1976). Because the nascent generative cell is equidistant from the two apertures, it obeys Huynh's "law of the longest distance" (Huynh, 1972; Sampson, 1982). The generative cell is soon detached from the wall of the grain to lie within the cytoplasm of the generative cell. In all three taxa the pollen is shed in the two-celled stage (FIGURES 50, 51).

The septum between each pair of microsporangia breaks down before dehiscence (FIGURE 43). Lateral longitudinal slits are formed, each by separation of small cells along a line of weakness (stomium) at the outermost part of the wall that separates radially adjacent microsporangia, and pollen is shed.

GYNOECIUM

TRIMENIA PAPUANA. The gynoecium consists of one (very rarely two) carpels. At anthesis the carpel is ca. 2 mm long and 1 mm broad. The barrel-shaped,

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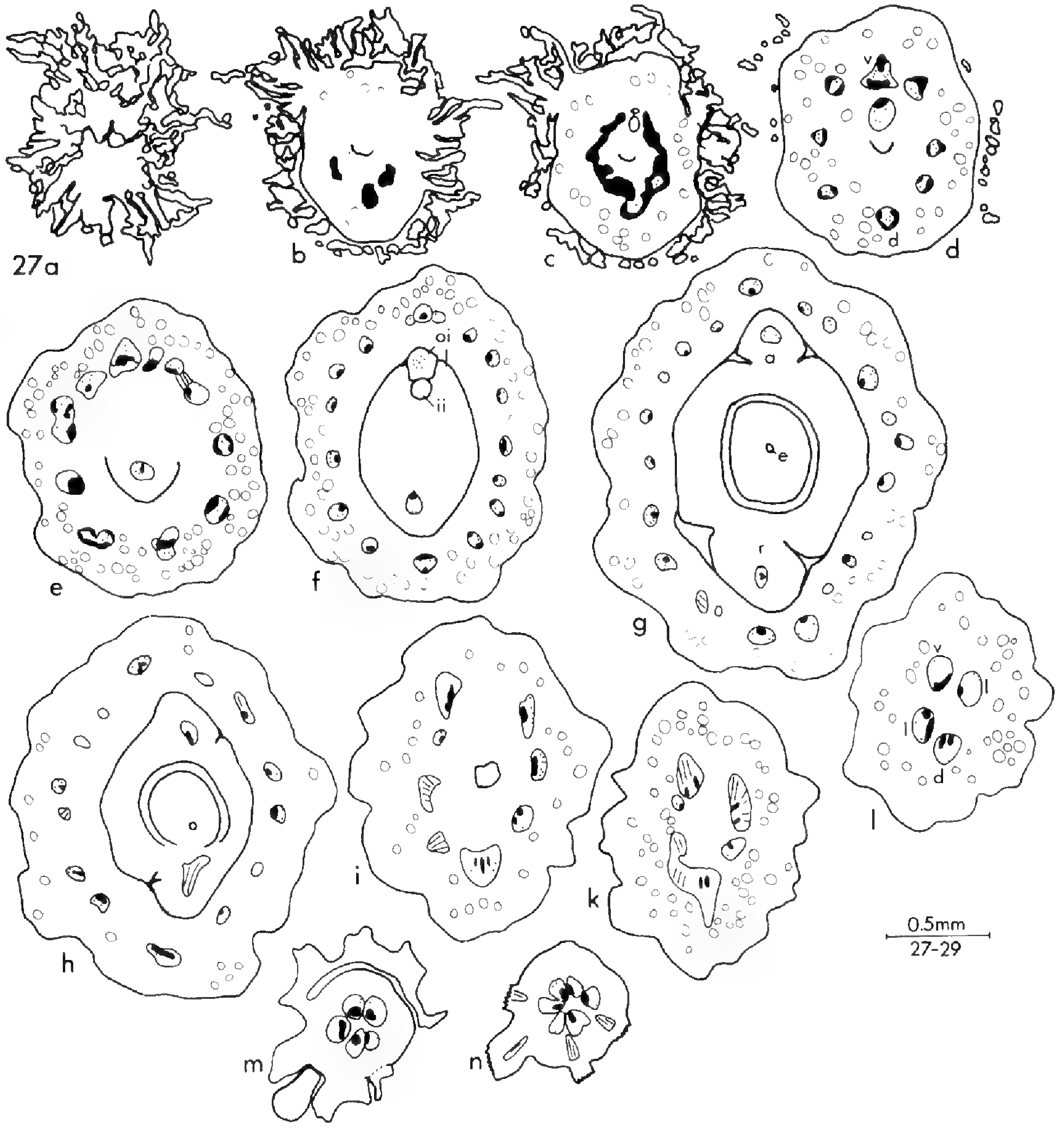
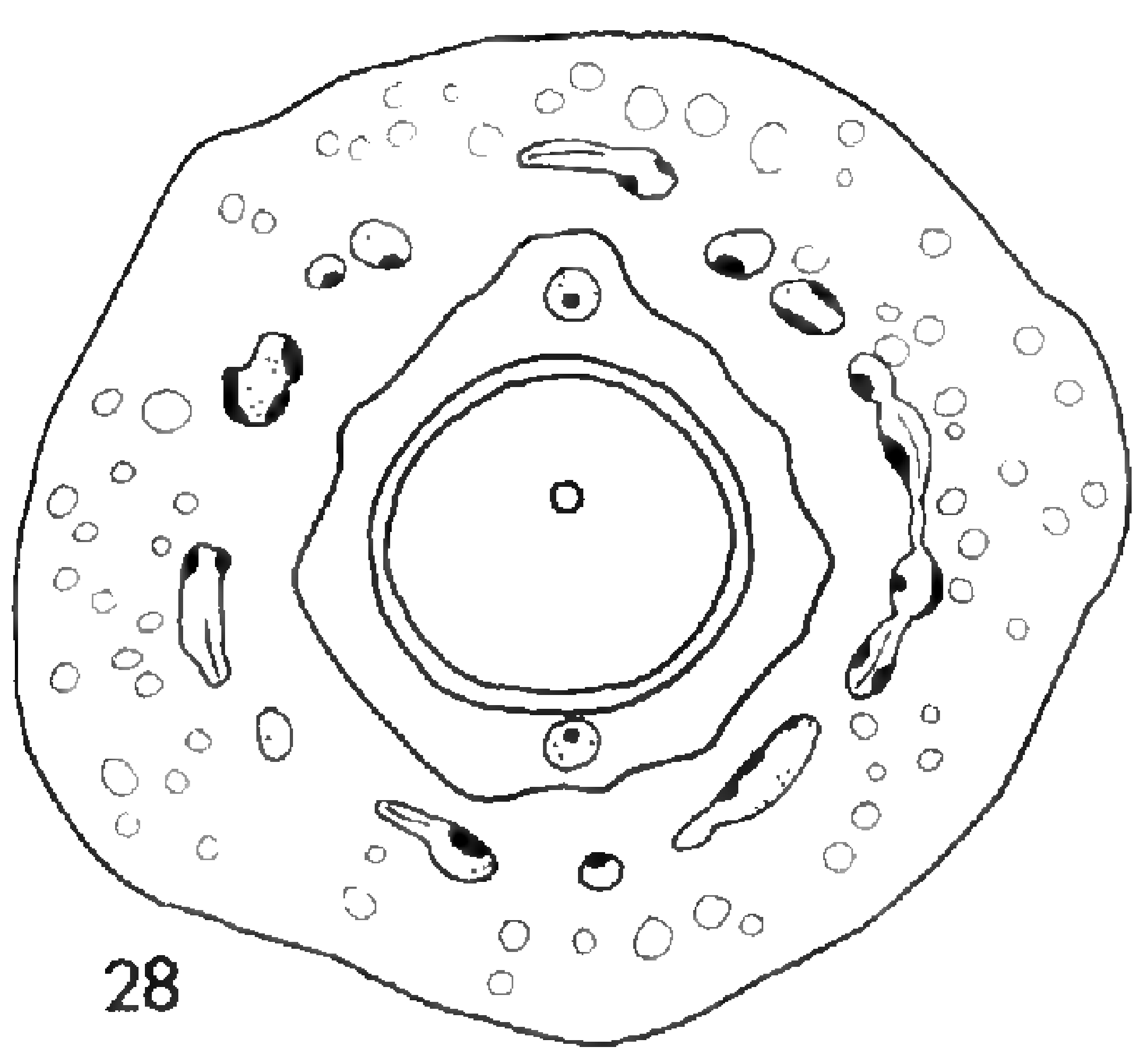
of epidermal origin indicated), inception of inner integument (*E 4087*); 23, rotation of ovule almost completed, ventral vascular bundle still procambial (*E 4087*); 24, stage with meiocytes in ovule, integumentary vascular bundle still procambial (cf. FIGURE 26) (*W,* 1970); 25, ovule at anthesis, elongated nucellus and long, tubular embryo sac (*W,* 1970); 26, nucellus with numerous meiocytes (enlarged from FIGURE 24) (*W,* 1970). (Dotted areas: meristematic tissue; procambium; phloem in differentiated vascular bundles. Black areas: xylem in differentiated vascular bundles. Plus signs: tanniferous tissue. Black lines in stigmatic region: cell rows.)

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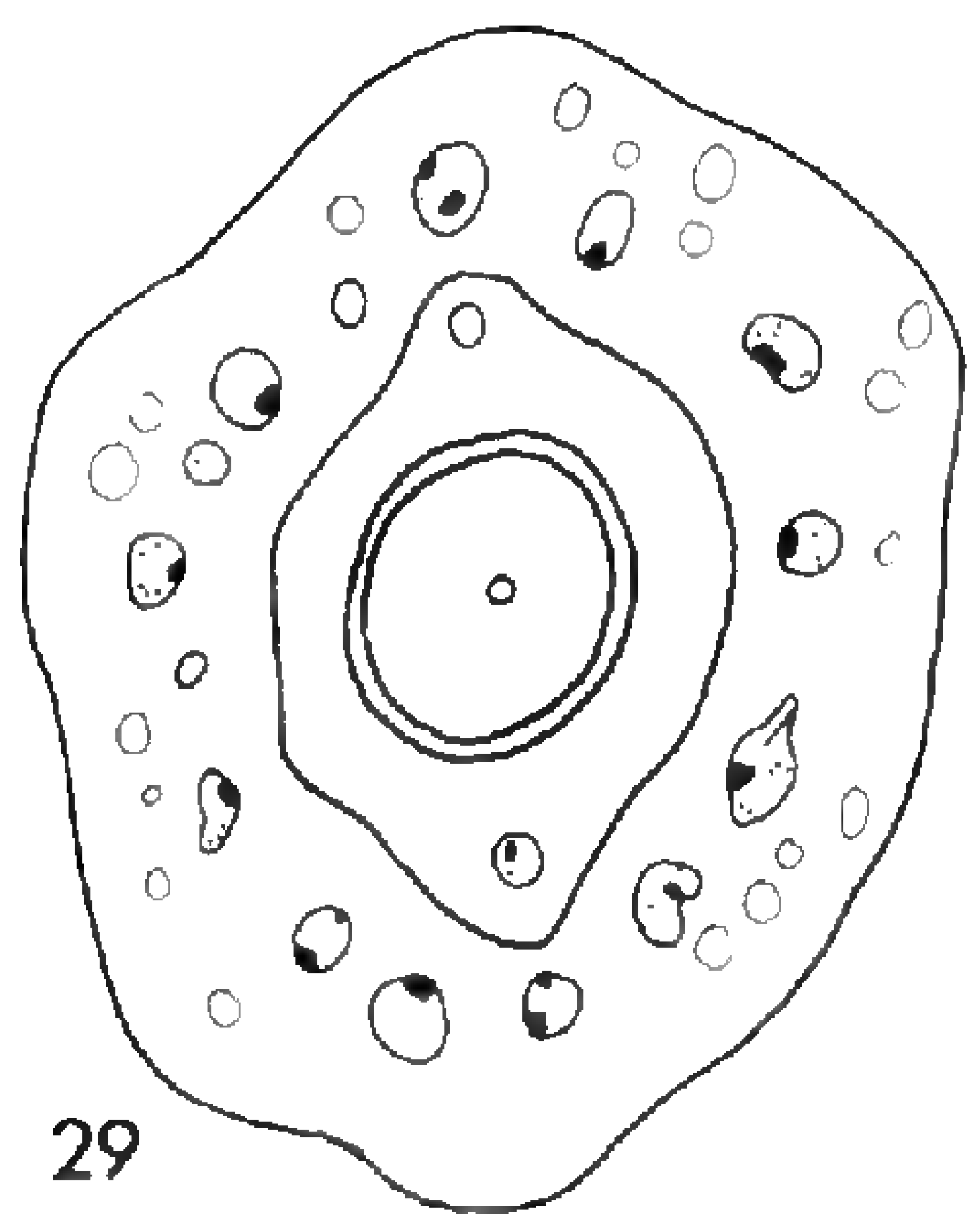
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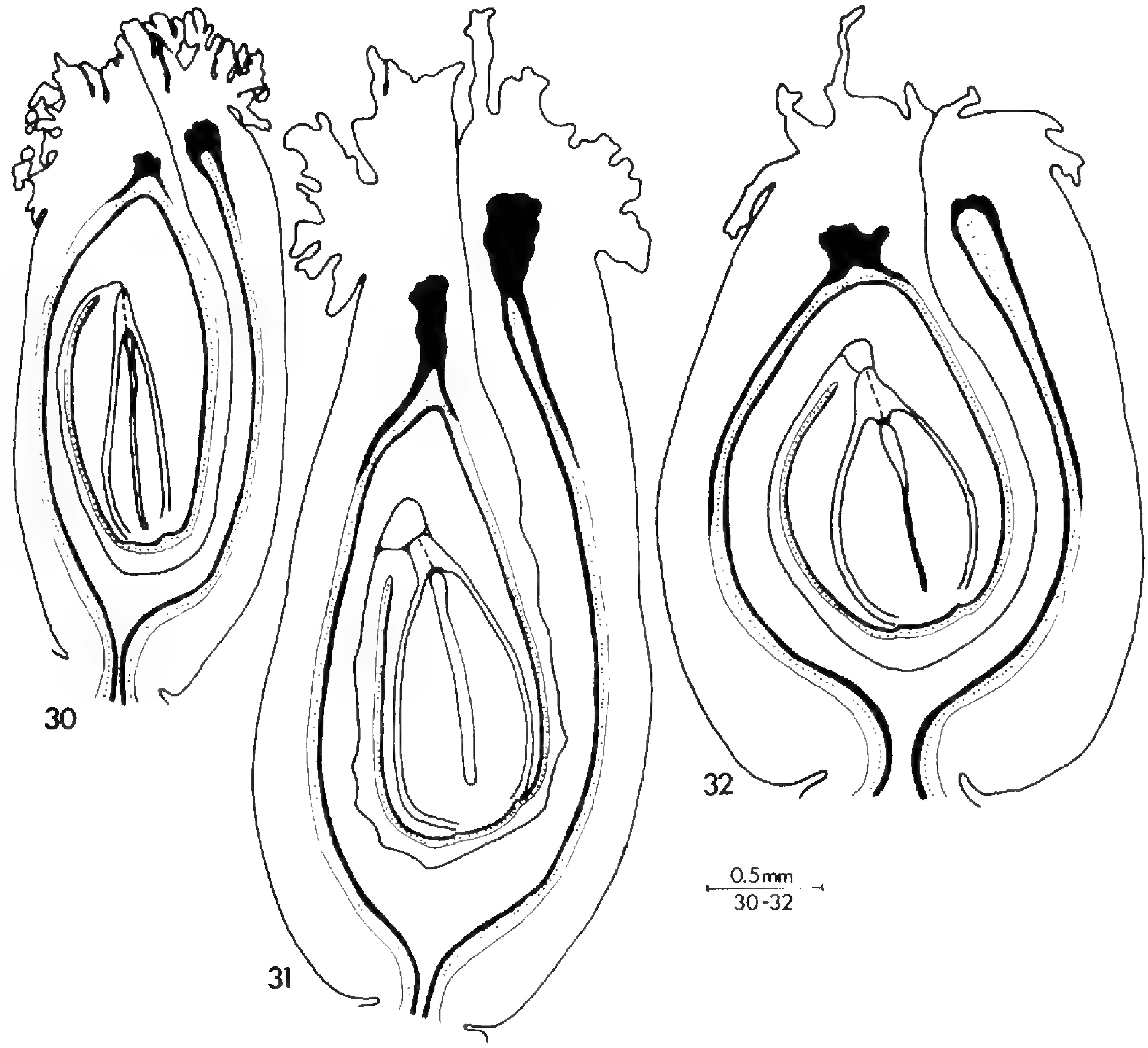
FIGURES 27–29. Transverse sections of carpels at anthesis (adaxial side up). 27, *Trimenia papuana* (*E 4066*), series from 1 carpel: a, stigma, "cross zone"; b, upper extension of dorsal bundle and 2 adjacent bundles; c, vascular bundles forming ring; d, e, top of



FIGURES 30–32. Median longitudinal sections of carpels at anthesis (left side = adaxial): 30, *Trimenia papuana* (*W*, 1970); 31, *T. neocaledonica* (*E 6315*); 32, *Piptocalyx moorei* (*E 4367*). (Dotted areas: phloem. Black areas: xylem.)

slightly asymmetric ovary is topped by a capitate, tuftlike stigma; there is no distinct style (FIGURES 1, 36, 63). The carpel is remarkable in being extremely utriculate (FIGURE 30). At anthesis the ventral and dorsal regions are nearly the same length. The ventral "cross zone" is situated at the top of the carpel in the stigmatic region (FIGURE 30). The "stylar" canal remains a narrow, transverse slit resulting from thickening but not widening of the carpellary wall (FIGURE 27, a–d). Longitudinal shallow furrows on the ovary surface mark the position of the anthers in bud. On the ridges between these depressions, rows

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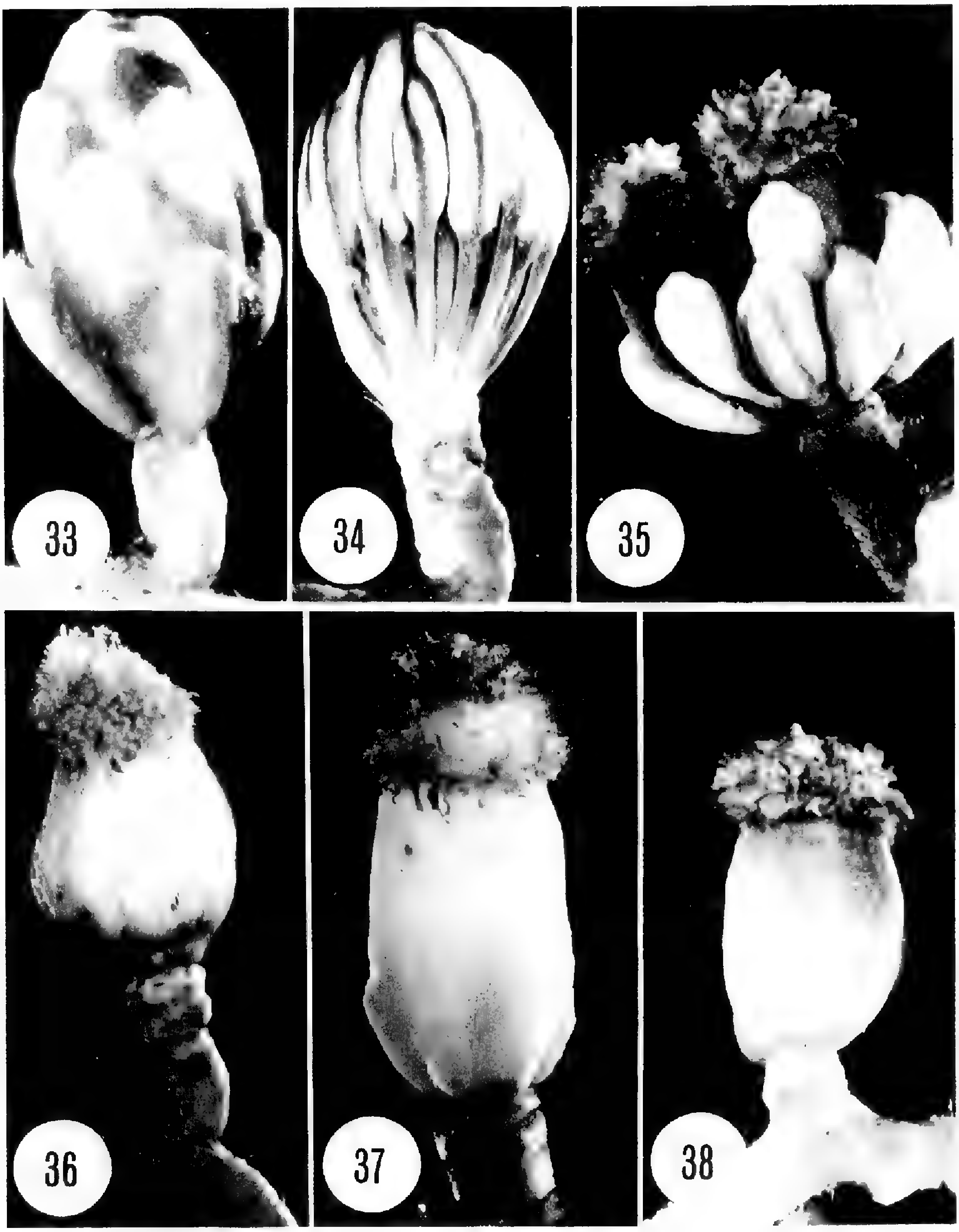
ovary; f, tip of outer (oi) and inner (ii) integuments; g, middle region of ovary (raphe (r) and antiraphe (a) separated from central body of ovule by deep furrows; embryo sac (e)); h, base of nucellus and integuments; i, base of ovarian cavity; k, l, union of vascular bundles into 1 dorsal (d), 1 ventral (v), and 2 laterals (l); m, base of ovary, rearrangement of carpellary bundles toward stele; n, level of androecium, stele with stamen traces. 28, *T. neocaledonica* (*E 6315*), middle region of ovary. 29, *Piptocalyx moorei* (*E 4367*), middle region of ovary, slightly earlier stage. (Dotted areas: phloem. Black areas: xylem. Small circles at periphery of sections: mucilage cells.)



FIGURES 33–38. Bud, flowers, and gynoecia, × 10. 33, *Trimenia papuana* (*E 4066*), mature bud, outermost tepals fallen. 34, *T. papuana* (*E 4066*), flower shortly before anthesis, tepals removed. 35, *Piptocalyx moorei* (*E 4367*), bicarpellate flower at early anthesis. 36–38, gynoecia after anthesis: 36, *T. papuana* (*E 4066*); 37, *T. neocaledonica* (*E 6315*); 38, *P. moorei* (*E 4367*).

of hooklike, upwardly directed, unicellular hairs are developed (FIGURES 60, 61). The carpel contains one ovule in a ventral-median position. The ovule is crassinucellar, bitegmic, anatropous, and pendent, with the micropyle directed upward (FIGURES 25, 27, 30, 64).

At anthesis a number of branching and anastomosing bundles (up to ten on each side) extend through the ovary wall between the dorsal and the ventral vascular bundles (FIGURE 27, g). They are more numerous than as described by Money, Bailey, and Swamy (1950, *table 3,* p. 389)—20 or more compared to four or five! The dorsal bundle terminates immediately below the stigma, and the other bundles are slightly shorter (FIGURE 27, b). The bundles all join near the top, forming a ring of short, tracheidlike cells (FIGURE 27, c). In the upper region of the carpel, each bundle has several tracheids on its outer side, while the normal xylem on the inner side is smaller (FIGURES 27, d; 30). Toward the base of the carpel, the lateral bundles anastomose, so that four more or less clear-cut complex bundles remain: a dorsal, a ventral, and two laterals (FIGURE 27, h–m). There is no obvious reorientation of the bundles demarcating the transition between the gynoecium and the floral stele, in contrast to the situation in many other plants.

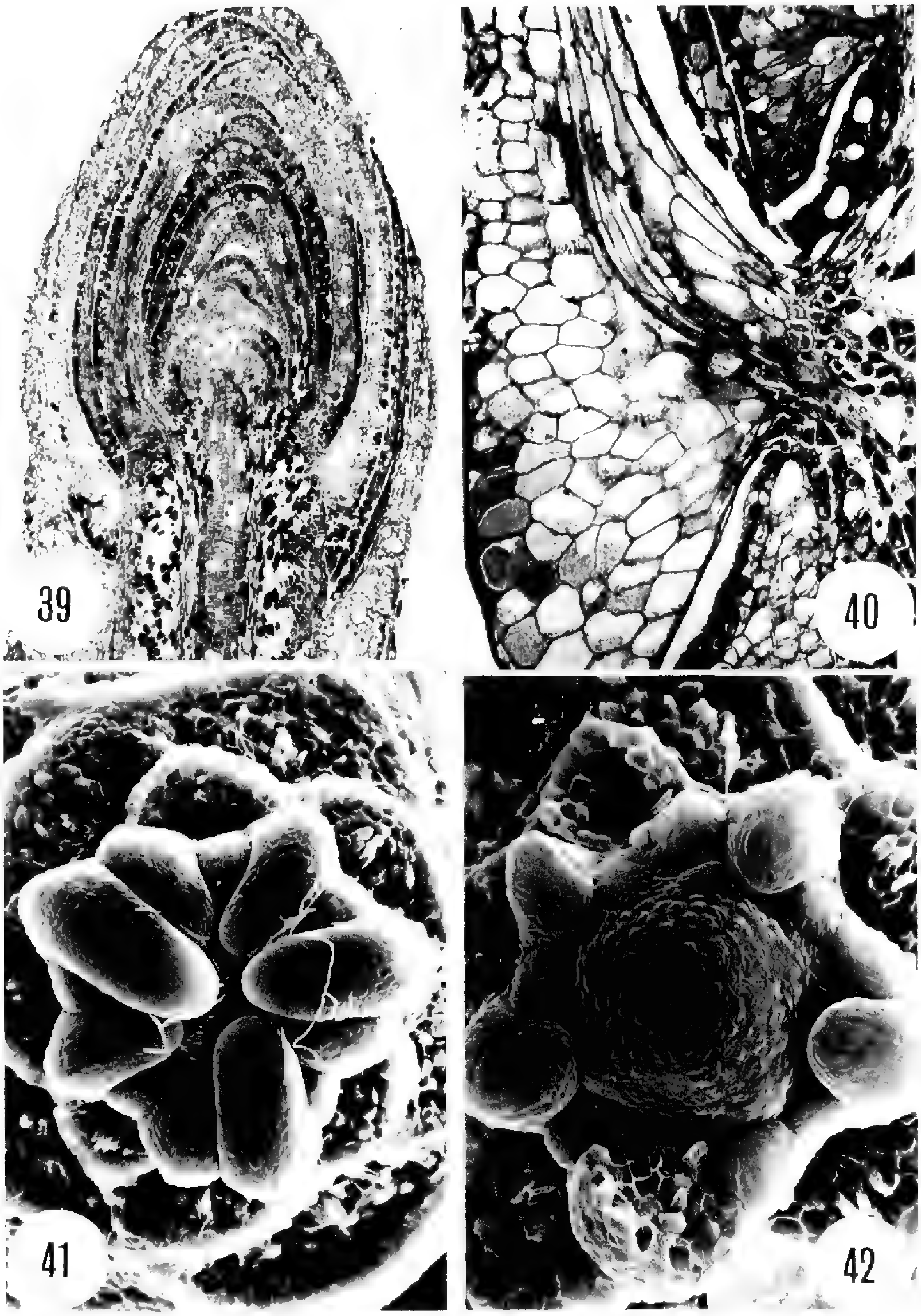
A strand from the ventral bundle supplies the ovule. The ovular bundle does not terminate at the chalaza but extends to the top of the outer integument near the micropyle (FIGURES 25, 27). Here, the outer integument has a very short, discrete tip (FIGURE 27, f). In the raphe and the outer integument (antiraphe) the vascular bundle occupies the peripheral region, which suggests that thickening of these parts occurs only on their inner side.

The inner integument is three or four cells thick. The outer integument is about six or seven cells thick, except at the top (ten to fifteen cells) and in the vascularized median region. There are three histologically conspicuous cell layers: the very small celled, "meristematic" inner epidermis of the ovary wall; the outer epidermis of the outer integument, with radially much elongated cells that develop into the stony layer of the seed; and the inner epidermis of the inner integument, which is tanniferous (FIGURE 25).

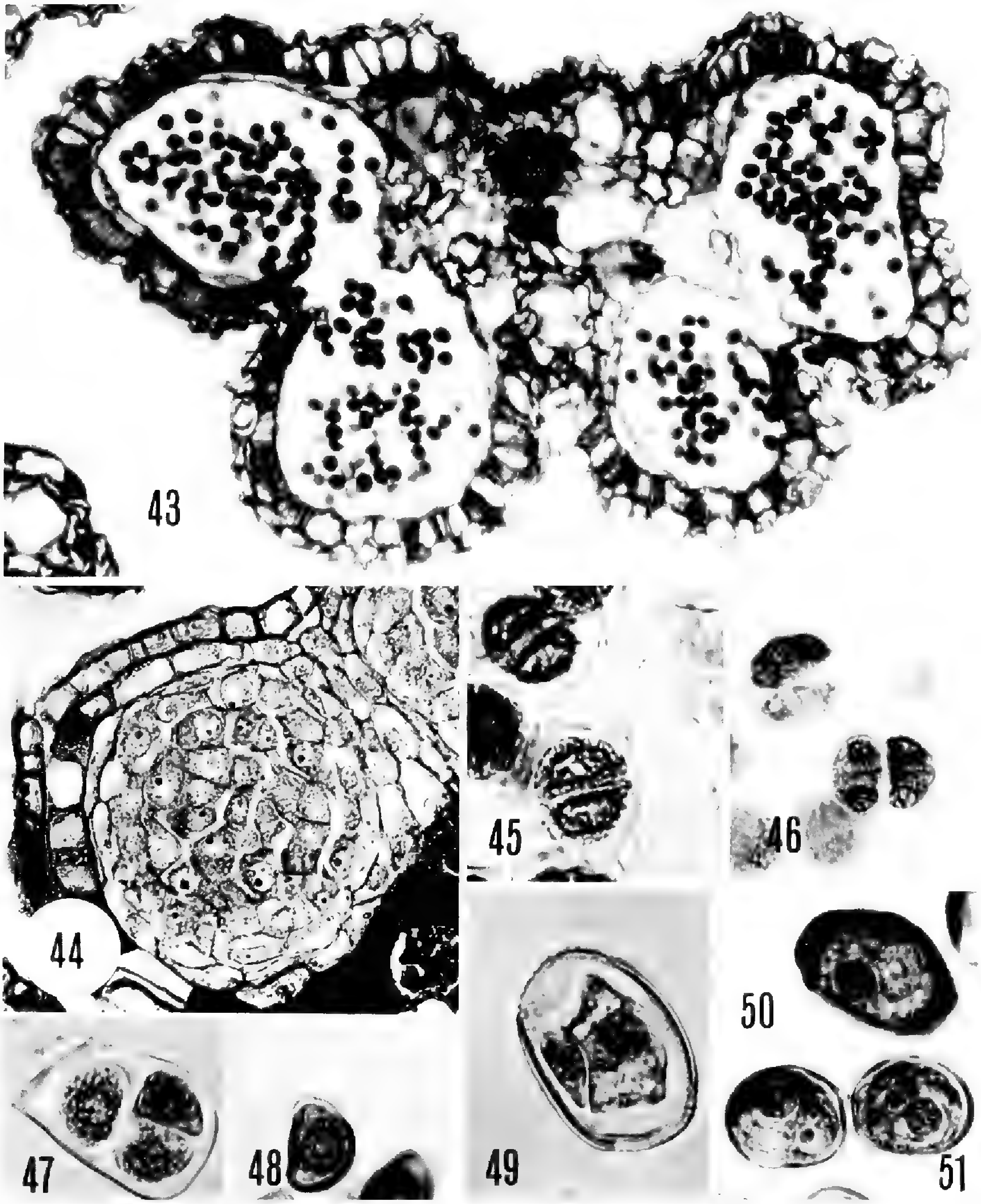
The ovule almost completely fills the ovary; the small gaps in between contain a mucilaginous secretion. In the middle region of the ovary, deep furrows separate the raphe and the antiraphe from the central portion of the ovule (FIGURE 27, g, h). The inner integument forms a massive cap over the micropyle, with the center containing a tanniferous zone (FIGURES 25, 64). The outer integument is also involved in micropyle formation. The long, narrow embryo sac extends throughout the entire length of the nucellus, almost growing out of the top of it (FIGURE 25).

The plumose stigma consists of long, pluricellular, pluriseriate, tanniferous hairs (FIGURE 62). The periphery of the carpel contains numerous large mucilage cells and—in the uppermost part—some groups of weakly lignified cells; the upper part of the center of the carpel (and ovular base) has especially thick-walled (but not lignified) cells with irregular thickenings. It seems unlikely, however, that this is pollen tube transmitting tissue because the cells are isodiametric, not elongated. Pollen tubes probably grow only through the narrow "stylar" canal. Together with the ovular surface, this tissue becomes lignified, beginning in its center, during fruit development.

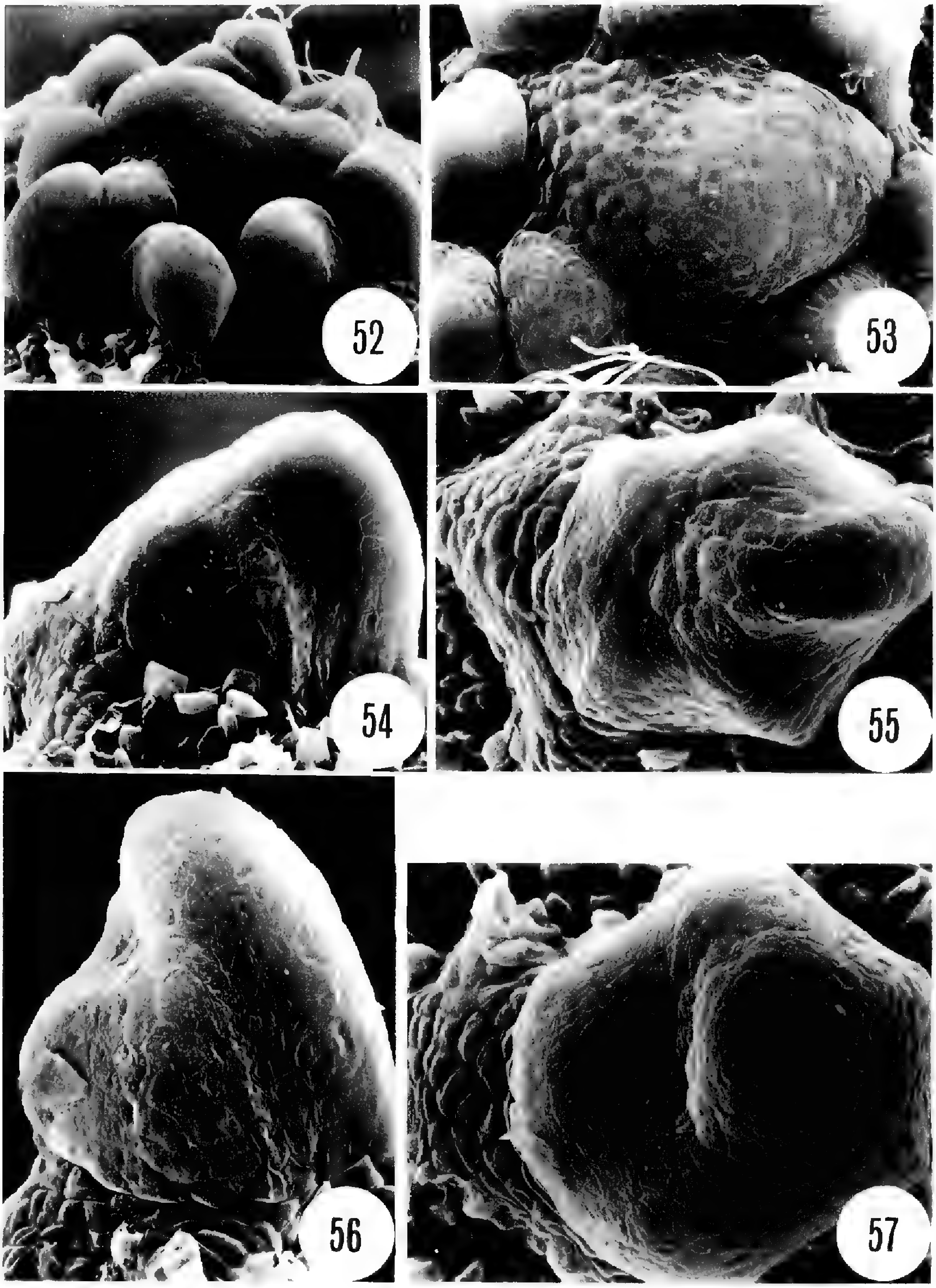
Soon after anthesis, the ovary wall interior to the vascular bundles becomes tanniferous. There is no further lignification in the ovary wall. The groups of



FIGURES 39–42. *Trimenia papuana.* 39, floral bud at time of androecium initiation (*E 4087*), median longitudinal section, × 40 (cf. FIGURE 8). 40, abscission of outer tepal from mature bud (*E 4066*), median longitudinal section (note dorsal extension), × 100. 41, 42, floral buds at time of initiation of inner stamens (*E 4087*), note spiral phyllotaxy: 41, tepals and few outermost stamens removed, × 120; 42, tepals and many outer stamens removed, × 200.



FIGURES 43–51. Anther and pollen development. 43, *Trimenia neocaledonica* (*E 6315*), transverse section through nearly mature anther, × 100. 44, *Piptocalyx moorei* (*E 4005*), portion of transverse section through young anther, showing microsporangium with sporogenous tissue, × 375. 45–48, *T. papuana* (*W,* 1970), × 800: 45, pollen mother cells at prophase II; 46, pollen mother cells at telophase II; 47, young tetrad with callose wall material enclosing microspores (only 3 visible); 48, young microspore soon after separation from tetrad. 49, *T. neocaledonica* (*M 4044*), pollen grain soon after formation of vegetative cell and generative cell (at left), × 800. 50, *P. moorei* (*E 4367*), mature pollen grain, × 800. 51, *T. papuana* (*E 4066*), mature pollen grains, × 800.



FIGURES 52–57. *Trimenia papuana* (*E 4087*). 52, 53, floral apex at time of carpel initiation: 52, lateral view, × 200, carpel primordium at left; 53, from above, × 330, carpel primordium at right. 54, 55, carpel primordium with ventral "cross zone" differentiated: 54, lateral view, × 360; 55, from above, × 410, note residual floral apex at left with convex cell surfaces. 56, 57, carpel primordium at chairlike stage: 56, lateral view, × 360; 57, from above, × 410.

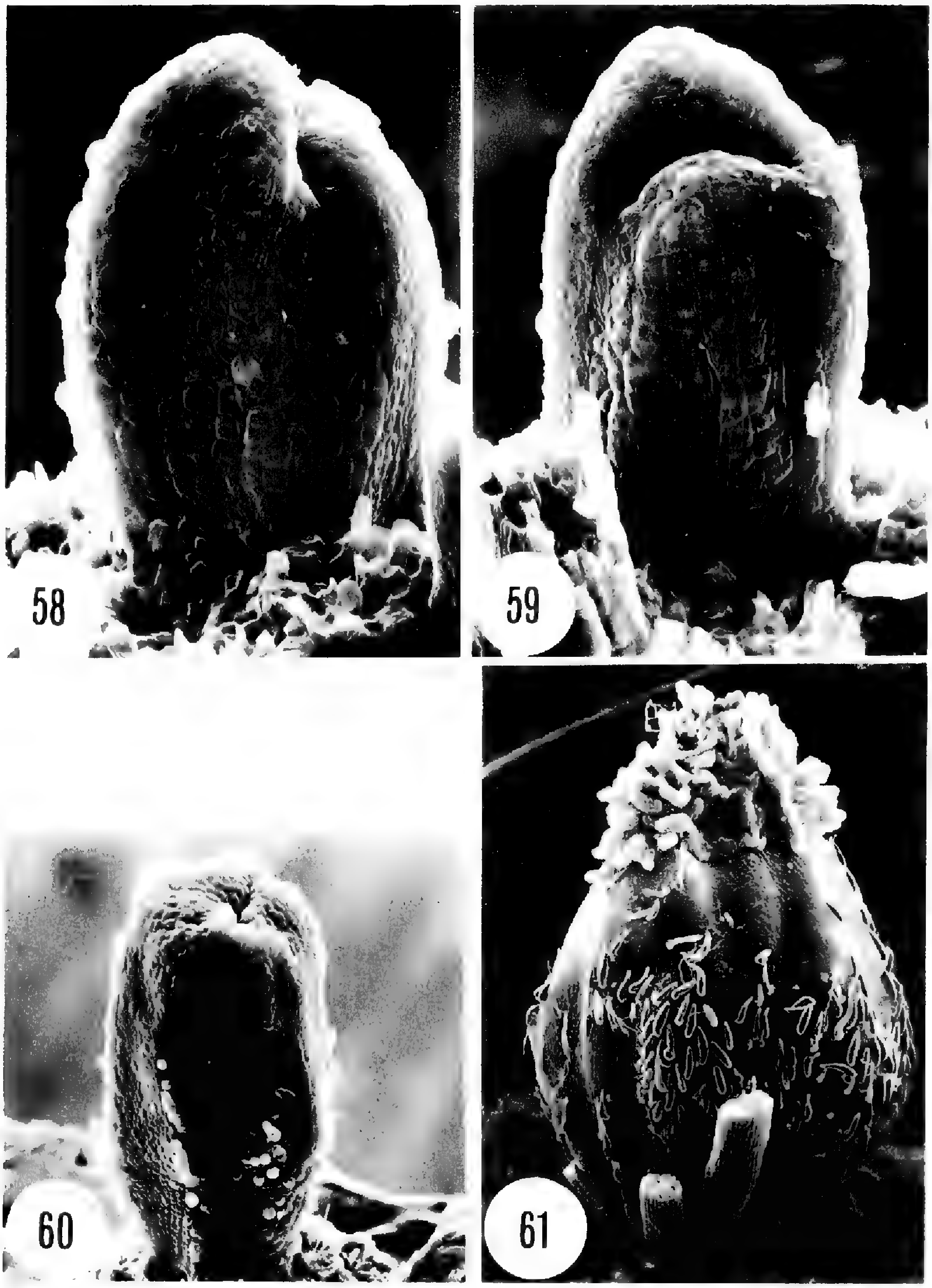
weakly lignified cells at the upper periphery of the carpel do not differentiate further.

The carpel is initiated at a normal divergence angle from the last stamen, to one side of the apex (FIGURE 53). Since a small portion of the ventral part of the apex is not used up during carpel formation, the carpel is not truly terminal. In SEM preparations the residual apex is distinguished by its convex cell surface; on the fast-growing carpel primordium the cell surface is flatter (FIGURES 52–57). Histologically, the residual apex soon becomes tanniferous (FIGURES 20, 21). The carpel primordium is thicker than a stamen primordium even at a morphologically undifferentiated stage (FIGURE 53). The carpel primordium soon becomes angled because of the protruding neighboring stamen primordia (FIGURES 55, 57). Halfway up its ventral side a platform ("cross zone") arises (FIGURES 20, 54), and the carpel primordium becomes chair shaped (FIGURES 21, 56). At this stage the carpel bears considerable resemblance to those of the Lauraceae (Endress, 1972) and certain Monimioideae of the Monimiaceae (Sampson, 1969a; Endress, 1980a). Unlike in the Lauraceae and the Monimioideae, however, during further development by extensive intercalary elongation, the relative difference in length between dorsal and ventral parts decreases, and the carpel becomes extremely utriculate (FIGURES 22–24, 58–60). There is an early inception of the pluricellular stigmatic papillae, coupled with (and even preceded by) extensive periclinal cell divisions of the epidermis in the apical part of the carpel (FIGURES 22, 23, 60). The stigma is conical in bud; only at anthesis does it expand and become capitate (FIGURES 61, 63).

By anthesis, the ovule has rotated almost 360° from the original ventral cross zone where it originated (FIGURES 21–25, 30). The inner integument appears before the outer, as is normal in bitegmic ovules (FIGURE 22). The nucellus undergoes relatively little growth until meiosis and is soon overtopped by the inner integument. This leaves only a narrow micropyle, which becomes indistinct even before anthesis (FIGURE 24).

At the time of integument initiation, the nucellar tissue consists of relatively small cells and an archesporium is not yet distinct. Later, numerous meiocytes differentiate at the base of the nucellus (FIGURES 24, 26, 64). Thus, the archesporium is multicellular. One or several embryo sacs start growing after meiosis, but only one reaches maturity. It grows like a narrow tube toward the apex of the now fast-elongating nucellus and stops immediately at the border of the nucellar apex, near the cap over the nucellus formed by the inner integument (FIGURE 25). There it becomes more voluminous. The egg apparatus and polar nuclei are situated near the nucellar apex, while the antipodals probably remain at the base of the embryo sac tube but are hard to trace. It appears as if the tanniferous hypostase and the tanniferous cap over the nucellus formed by the inner integument prevent further elongation of the intrusive embryo sac apices at both ends of the nucellus.

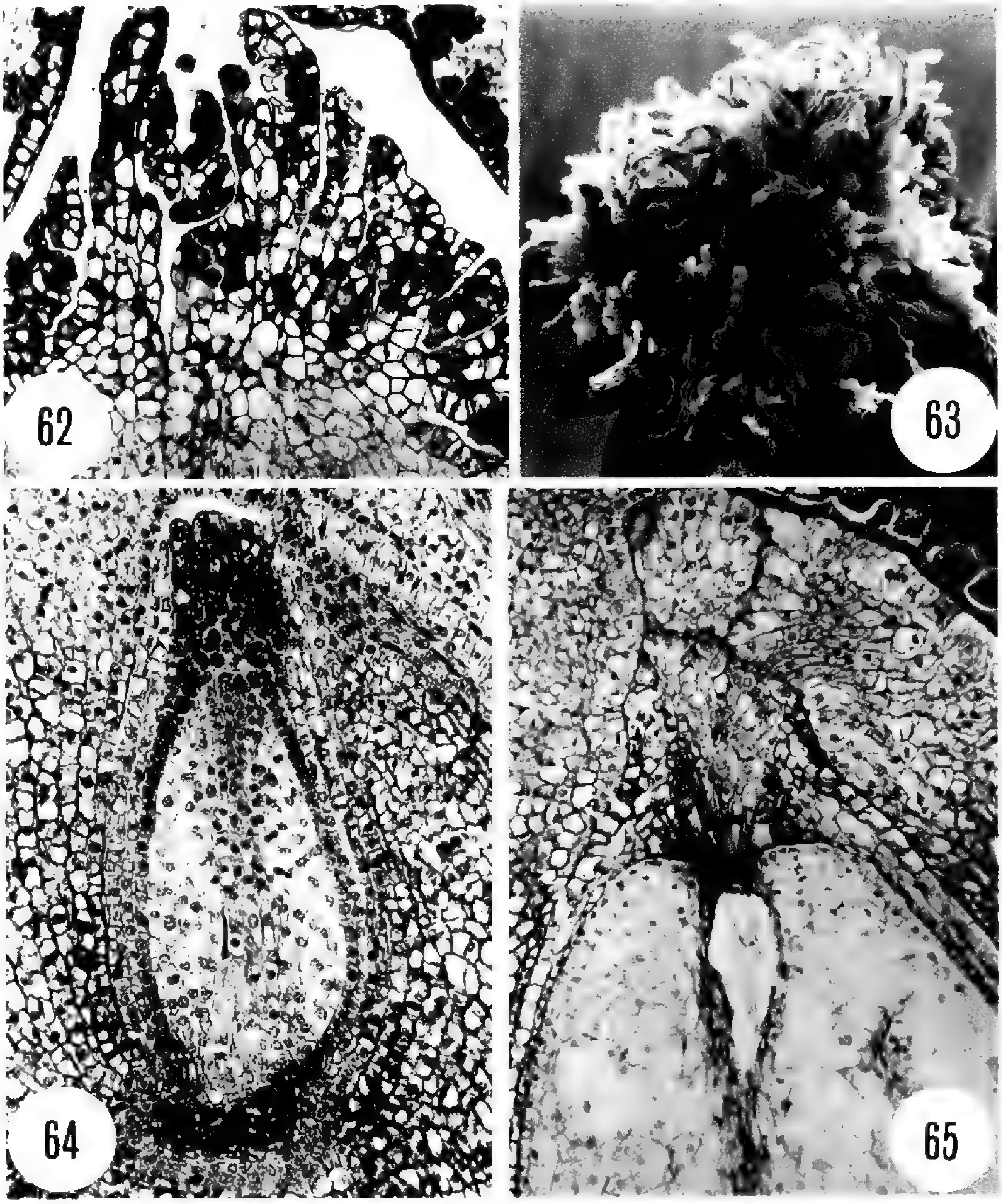
OTHER SPECIES. The gynoecial structure of *Trimenia neocaledonica* and *Piptocalyx moorei* closely resembles that of *T. papuana* (FIGURES 31, 32). Therefore, only differences will be mentioned.



FIGURES 58–61. *Trimenia papuana.* 58, 59, young carpel after intercalary longitudinal growth of middle and basal regions, × 220 (note longitudinal cell "families"): 58, lateral view; 59, from adaxial side. 60, young carpel at inception of stigma differentiation (*W,* 1970), × 80. 61, carpel with conical stigma, from older bud (*E 4066*), × 30.

In *Trimenia neocaledonica* the carpel at anthesis is longer (ca. 3 mm) than in *T. papuana* (FIGURES 31, 37). Histologically, the whole carpel is richer in tannins; the mucilage cells at the carpel periphery are larger, and their mucilage content seems to be higher (FIGURE 28). The ovule is thicker than in *T. papuana.*

In *Piptocalyx moorei* the carpel is ovoid and thicker (ca. 1.5–2 mm) but not



FIGURES 62–65. Stigmas and ovules. 62–64, *Trimenia papuana:* 62, stigma from old bud (*E 4066*), longitudinal section, × 100 (note pluricellular papillae); 63, stigma at anthesis (*E 4066*), × 30; 64, ovule with several meiocytes (*W,* 1970), median longitudinal section, × 160 (note tanniferous tissue in top of inner integument and hypostase). 65, *Piptocalyx moorei* (*E 4367*), ovule at anthesis, longitudinal section, × 120, nucellar apex depressed and with papilla, embryo sac apex inside papilla.

longer than in *Trimenia papuana* (FIGURES 32, 38). Histologically, the tannin content is lower. There are fewer (but larger) mucilage cells (FIGURE 29). In the upper carpel wall the outer tracheid zone of the vascular bundles is even more developed than in *T. papuana.* The most obvious difference in the ovular structure at anthesis is that the nucellar apex is depressed, and in the center of this depression the tip of the ripe embryo sac is situated inside a papilla (FIGURES 32, 65). The inner integument contains conspicuously elongated cells near the depression. In both species the ovary walls are glabrous, in contrast to those of *T. papuana.*

DISCUSSION

STRUCTURE OF FLORAL ORGANS

PHYLLOTAXY, NUMBER, AND INITIATION OF FLORAL PARTS. The floral organs have a spiral phyllotaxy in all four species examined. This has not been recognized in earlier studies. While some authors (Perkins & Gilg, 1901; Gibbs, 1917; Perkins, 1925; Rodenburg, 1971) report a spiral perianth for *Trimenia* species, only Morat and MacKee (1977) state that the androecium has a spiral phyllotaxy (in *T. neocaledonica*). The reason is that the spiral is obscured during later ontogeny because of differential expansion of the flower base caused by the extensive enlargement of the carpel. In *Piptocalyx* spiral floral phyllotaxy has not previously been recognized.

The analysis of floral parts in our material has extended the previously recorded range of variation in stamen number in all species, and in tepal number in all species except *T. weinmanniifolia* (Rodenburg, 1971; Beadle, 1972; Morat & MacKee, 1977). *Trimenia neocaledonica* has invariably been described as having 12 stamens, even in the recent studies of Rodenburg (1971) and Morat and MacKee (1977). In our material it varied from 11 to 15, with an average of 13.2.

Thus, the family Trimeniaceae is an additional one within the Magnoliidae to have spiral floral phyllotaxy (cf., for example, Endress, 1980a, 1980b). In all these cases there tends to be an obvious correlation between spiral phyllotaxy, marked plastochrons, and considerable variation in the number of floral parts.

PERIANTH. In the Trimeniaceae, as in other Magnoliidae with spiral floral phyllotaxy, there is neither a separation into perianth members and bracts toward the floral periphery nor a clear differentiation of two different kinds of perianth organs—sepals and petals (see also Hiepko, 1965; Endress, 1980a, 1980b).

ANDROECIUM. Stamen structure is unremarkable. The stamens have neither the valvular dehiscence and paired appendages typical of the Laurales nor a massive construction as in many Magnoliales; they are differentiated into filament and anther. The shape of the long, slender anthers and thin filaments of some *Trimenia* species is unusual and resembles that of many wind-pollinated groups in various angiosperm families (e.g., Eupteleaceae; cf. Endress, 1969).

The Trimeniaceae differ from the Chloranthaceae (Vijayaraghavan, 1964), the Lauraceae (Bhandari, 1971), the Monimiaceae (Sampson, 1969a, 1969b; Bhandari, 1971), and most other members of the woody Ranales in having a middle wall layer only one or two cells in thickness. In having a glandular tapetum the Trimeniaceae resemble the Calycanthaceae (Bhandari, 1971), the Chloranthaceae (Vijayaraghavan, 1964), *Cassytha* of the Lauraceae (Sastri, 1963), and the Monimiaceae. This contrasts with other members of the Laura-

TABLE 1. **Similarities between four species of Trimeniaceae.**

	Species			
Character	*Trimenia papuana*	*T. weinmanniifolia*	*T. neocaledonica*	*Piptocalyx moorei*
HABIT	Tree			Vine
TEPAL NUMBER	≥ 11			≤ 11
NUCELLAR APEX	Not depressed			Depressed
LEAF MARGINS	Toothed		Entire	
INFLORESCENCE TYPE	Compound botryoids (panicles)		Simple botryoids	
FLOWER BUD SHAPE	Elongate		Globular	
TEPALS				
VASCULARIZATION	One bundle		Bundle branching	
INNERMOST, SHAPE	Spathulate		Obovate	
OUTER, SHAPE	Markedly hypopeltate		Weakly hypopeltate	
ANTHER DEHISCENCE	Latrorse		Extrorse	
POLLEN	Polyforate or inaperturate		Disulculate	

ceae, which have an amoeboid tapetum (Sastri, 1963). Successive cytokinesis, recorded in microspore mother cells of the Trimeniaceae, has also been found in some Monimiaceae (Sastri, 1963; Sampson, 1969a, 1977) and in the Lauraceae (Bhandari, 1971); simultaneous cytokinesis has been found in another member of the Monimiaceae (Sampson, 1969b) and in the Calycanthaceae (Bhandari, 1971) and Chloranthaceae (Vijayaraghavan, 1964). As is characteristic of the more primitive groups of angiosperms (Brewbaker, 1967), the Trimeniaceae shed pollen in the two-celled condition, although three-celled pollen has been found in one genus of the Lauraceae (Gardner, 1974) and in one member of the Monimiaceae (Sampson, 1969b).

GYNOECIUM AND FRUIT. The mature carpel is totally utriculate up to the stigma. This was inferred by Leinfellner (1969) from the description of the vasculature in Money, Bailey, and Swamy (1950) and is confirmed in this study. However, the vasculature of the carpel at anthesis is more complicated in *Trimenia papuana* and the two other species investigated than was described by Money, Bailey, and Swamy. Furthermore, they did not report the presence of a vascular bundle in the outer integument.

A remarkable morphogenetic feature is that in spite of the fully utriculate condition of the carpel at anthesis, the early developmental stages are relatively less utriculate and thus more closely resemble those of the Lauraceae and some Monimiaceae (Sampson, 1969a; Endress, 1972, 1980a). The Trimeniaceae are therefore one more example of a family in the Magnoliidae with extremely utriculate carpels (see, for example, Endress, 1980b).

The ovule of the Trimeniaceae has several peculiar lauralian traits that it shares especially with certain Lauraceae, Hernandiaceae, and Calycanthaceae, but (interestingly) less with the Monimiaceae. However, only a few representatives of these families have been studied so far (see TABLE 2, and Endress, 1972), and it is not known how widely distributed these traits are within the Laurales. Such features are the differentiation of many meiocytes in the nucellar base, the marked elongation of the nucellus after meiosis, the apical depression of the nucellus, and the tubelike, intrusive growth of the embryo sac toward

TABLE 2. **Occurrence in related families of characters found in the Trimeniaceae.***

CHARACTER OF TRIMENIACEAE	RELATED FAMILIES			
	Lauraceae	**Chloranthaceae**	**Hernandiaceae**	**Monimiaceae, s.l.**
Climber (*Piptocalyx*)	(*Cassytha*)	−	(+)	(*Palmeria*)
Leaves opposite	(+)	+	−	+
Node unilacunar, 2-trace	+	+	−	−
Mucilage cells present (L)	+	−	(+)	−
Anemophily	−	(+)	−	(*Hedycarya*, p.p.?)
Floral phyllotaxy spiral	−	−	−	(+)
Stamen without appendages	−	+	(+)	(+)
Anther dehiscence longitudinal	−	+	−	(+)
Tapetum glandular	(*Cassytha*)	+	?	+
Pollen meiosis successive	+	−	?	(+)
Pollen inaperturate (*Trimenia*, p.p.) (Walker, 1976) (L)	+	(+)	+	+
Exine tectate-columellate (Sampson & Endress, in press; Kubitzki, 1981)	−	+	−	(*Laurelia*)

Carpel 1 per flower	+	+	+	(*Xymalos*)
Carpel extremely utriculate at anthesis	–	(+)	–	–
Carpel development including chairlike stage	+	+	?	(Monimioideae)
Ovule 1 per carpel, in ventral-median position (L)	+	+	+	+
Ovule anatropous, pendent (L)	+	–	+	(Monimioideae)
Outer integument with vascular bundle (Van Heel, 1971)	–	–	(*Hernandia*)	–
Exotesta with palisade-shaped cells (Corner, 1976)	(*Cassytha* and other genera)	–	–	–
Fruit: berry	(+)	–	–	–
Nucellus elongated (L)	+	–	(+)	–
Nucellar apex depressed (*Piptocalyx*)	(*Cassytha*)	–	(*Gyrocarpus*)	–
Meiocytes several per ovule (L)	(*Cassytha*)	–	?	(*Siparuna*)
Embryo sac narrow, tubular (L)	+	–	+(?)	(*Siparuna*)
Chromosome number $n = 8$ (Goldblatt, 1974; Goldblatt & Briggs, 1979; Ehrendorfer, 1976; Raven, 1976)	–	(*Hedyosmum*)	–	–

*References are not given for characters reviewed in Money, Bailey, and Swamy (1950) and Endress (1972) or discussed elsewhere in this paper.

Explanation of symbols: L, characteristic "lauralian" feature; +, present; (+), sometimes present; –, absent; ?, unknown.

the nucellar apex (and eventually into the micropyle in other Laurales). These features seem to be less prominent in the Magnoliales.

The fruits of the Trimeniaceae have variously been described as berries (e.g., Rodenburg, 1971) or drupes (e.g., Morat & MacKee, 1977). This may be partly because the term "berry" is not always used in the same sense, but it is also due to misinterpretation of the fruit. The fruit contains a hard layer that is grooved or ridged on the outer surface in some species. Although the hard layer looks like the endocarp of a drupe, it clearly corresponds to the periphery of the seed. The fruit is, therefore, a one-seeded berry.

SYSTEMATIC CONCLUSIONS

RELATIONSHIPS WITHIN THE FAMILY. *Trimenia* and *Piptocalyx* were last compared by Gilg and Schlechter (1923). According to their key, *Trimenia* has 15 to 20 spiral tepals, *Piptocalyx* 4 to 6 biseriate ones. The present study has shown that the two genera are less distinctive in these features. Both have spiral tepals, and in rare cases *Piptocalyx* may have as many as 11, therefore reaching the lower limit of the tepal range of *T. papuana,* as given by Rodenburg (1971).

Another surprising result is that *Trimenia neocaledonica* shares some features with *Piptocalyx* that it does not share with the other *Trimenia* species. In particular, the discovery that the pollen of *T. neocaledonica* is disulculate as in *Piptocalyx* (not polyforate or inaperturate as in the other *Trimenia* species) is of interest in this context (Sampson & Endress, in press). Thus, *T. neocaledonica* clearly occupies a central position within the family. This is shown by TABLE 1.

It seems, therefore, that the only obvious differences left between *Trimenia* and *Piptocalyx* are growth form (tree vs. vine) and tepal number ($\geq$ 11 vs. $\leq$ 11).

From these results three possibilities for a classificatory consequence arise: the transfer of *Trimenia neocaledonica* to the genus *Piptocalyx,* the merger of *Piptocalyx* with *Trimenia,* or no change. The justification for following any of these three possibilities is about equal. We prefer the third possibility because it avoids unnecessary nomenclatural changes.

On the whole, the Trimeniaceae appear to be a rather uniform family. *Trimenia neocaledonica* is possibly the most primitive species.

RELATIONSHIPS WITH OTHER FAMILIES. Until the classic study on the Monimiaceae by Money, Bailey, and Swamy (1950), *Trimenia* and *Piptocalyx* were usually included in that family. Money, Bailey, and Swamy discussed the reasons for segregating these two genera into a separate family (following Gibbs, 1917) and found relationships with the Lauraceae, *Austrobaileya,* and the Chloranthaceae, in addition to the Monimiaceae. Thorne (1976) pointed to rather close relations with the Chloranthaceae; Takhtajan (1980), with the Amborellaceae. Dahlgren (1980) listed the Trimeniaceae between the Austrobaileyaceae and the Monimiaceae, and Cronquist (1981) placed them between the Amborellaceae and the Monimiaceae.

The results of our study underline the isolated position of the Trimeniaceae. The family shows relationships with the Lauraceae (especially the Cassythoideae), the Chloranthaceae, and the Monimiaceae, but it is only distantly related to the Austrobaileyaceae. The Amborellaceae are still not well enough known for a comparative evaluation. The Hernandiaceae also share a number of special characters with the Trimeniaceae. Those of particular interest are listed in TABLE 2.

That the Trimeniaceae belong to the Laurales is shown by some characteristic "lauralian" features (see TABLE 2). The core of the Laurales consists of the Monimiaceae, Lauraceae, Hernandiaceae, and Gomortegaceae.

However, several characters deviating from those generally found in the Laurales point to the isolated position of the Trimeniaceae. These characters include absence of a floral cup; spiral floral phyllotaxy—also present in Gomortegaceae and some Monimiaceae; caducous tepals; stamens without flaps and appendages—also present in some Monimiaceae; extremely utriculate carpels; polyforate pollen; tectate-columellate exine—also present in *Laurelia*; capitate stigma with multicellular papillae; outer integument with vascular bundle—also present in *Hernandia*; chromosome number of $n = 8$. Although the Trimeniaceae share a few of these characters with the Magnoliales, their affinities to the Laurales are still stronger, in spite of their isolation. A closer relationship with the Austrobaileyaceae, as supposed by some authors, can be excluded because the common shared features (vine, leaves opposite, node unilacunar and two-trace, floral phyllotaxy spiral, carpels extremely utriculate, outer integument with vascular bundle) are too scattered. The Austrobaileyaceae are of clearly magnolialian (not lauralian) affinity (Endress, 1980b).

Thus the Trimeniaceae are a very homogeneous, isolated relict family of the Laurales with closest relationships to the Lauraceae, Monimiaceae, Chloranthaceae, and Hernandiaceae; at the same time they are somewhat distant in certain characters from the core of the Laurales.

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P. K. E.
INSTITUT FÜR SYSTEMATISCHE BOTANIK DER UNIVERSITÄT
ZOLLIKERSTRASSE 107
8008 ZÜRICH, SWITZERLAND

F. B. S.
BOTANY DEPARTMENT
VICTORIA UNIVERSITY OF WELLINGTON
PRIVATE BAG
WELLINGTON, NEW ZEALAND

INBREEDING DEPRESSION IN METASEQUOIA

JOHN KUSER

EVER SINCE specimens of dawn redwood, *Metasequoia glyptostroboides* Hu & Cheng, grown from the Arnold Arboretum's 1948 seed introduction began to bear both microsporangiate and megasporangiate strobili (cones), there has been speculation as to whether the species would show inbreeding depression (U.S.D.A., 1974). Common symptoms of this phenomenon in conifers are reduced seed set and lowered vigor of progeny after selfing (Wright, 1976). This question is pertinent to *Metasequoia* because many of the trees now bearing cones are large, isolated specimens. Occasional seedlings have been raised from them, but viable seeds have been few (Wyman, 1968).

In the future it may be desirable to propagate the species from seed rather than from cuttings (as is usually done now), both for economy and to maintain genetic variability (Henkel, pers. comm.). It would be useful to identify the parent trees producing seed yielding the highest germination percentages and the most vigorous seedlings.

Because isolated specimens (400 m or more from the nearest other matûre specimen) presumably have no means to produce fertile seed except through self-pollination or apomixis, it was possible to use a simple strategy to test for inbreeding depression and to identify the most desirable parent trees: comparison of seed and seedling characteristics from a sample of isolated trees with those from a sample of trees in mixed-clone groves where cross-pollination is likely. The characteristics chosen for testing were weight and germination percentage of cleaned seeds, rate of seedling growth, mortality, and evidence of abnormalities associated with reduced growth.

At the same time, optimum conditions of temperature and light for germination could also be determined by testing several different environments.

MATERIALS AND METHODS

CONES AND SEEDS. In November, 1981, 200 to 250 cones were collected from isolated trees (nos. 1–4, TABLE 1) and from trees in mixed-clone groves (nos. 5–9). Twenty cones from each tree were measured and weighed, and seeds of 10 cones from each tree were carefully removed and counted. The remaining cones were dried for a week at ambient indoor temperature and the seeds removed.

Seeds were cleaned in a General blower (manufactured by New Brunswick Sheet Metal Works, New Brunswick, New Jersey) at the U.S.D.A. Federal Seed Laboratory, New Brunswick, New Jersey. The upward velocity of the vertical air column that the seeds entered was adjusted by trial and error until nearly

Journal of the Arnold Arboretum **64:** 475–481. July, 1983.

all filled seeds were accepted and nearly all empty ones were rejected. Each seed was examined in a diaphanoscope at magnifications of 7 to 10 × to check for presence of an embryo. From 30 to 300 seeds from each tree were counted, weighed, and placed on wet blotting paper in transparent plastic Petri dishes in a Pfeiffer Model 1C-D1 Daylight Seed Germinator. A 20°/30°C thermoperiod was used, with 16 hours at 20°C in darkness and 8 hours at 30°C with light. Germinants were counted every few days from the time germination began until it appeared to be complete.

Seeds of trees nos. 7 and 9, the two lots with the highest germination percentages, were then used to test five different germination environments: constant 15°C in darkness, constant 20°C with lights on 8 hours per day, 15°/25°C with lights on for 8 hours per day at 25°C, 20°/30°C as described above, and 20°/35°C with lights on for 8 hours per day at 35°C. Germinants were counted every few days until germination appeared complete.

To determine if all seeds containing live embryos were germinating under the test conditions (and by inference, whether stratification or chemical treatment could improve germination), samples from seedlots of trees nos. 5, 7, and 8 were cleaned in the blower at high air velocity, and then each sample was divided into two equal halves. One half was tetrazolium tested for live embryos, while the other was germination tested at 20°C. As a further check, seeds that had not germinated after 17 days were tetrazolium tested.

After testing of lots nos. 1 to 9 was complete, seeds from an additional grove tree and an additional isolated tree were received from Auburn, Alabama. These seedlots were added to the test because of their different geographic origin and their possibly different environmental conditions at pollination time, and in an attempt to obtain more "selfs."

SEEDLINGS. Seedlings from the three isolated trees that produced fertile seed were grown for comparison with seedlings from grove trees. Germinants to be tested were taken from the Petri dishes, potted in peat cubes, and replaced in the germinator for a week. They were then moved to a greenhouse at Cook College, New Brunswick, New Jersey, where they were grown under ambient daylight plus four hours of extra light supplied by cool-white fluorescent tubes between 10 P.M. and 2 A.M. nightly. Minimum night temperature was 18.3°C. When the seedlings had six to eight true leaves, they were moved to four-inch clay pots and transferred to another greenhouse with no supplemental light and a minimum night temperature of 15.6°C. They were watered daily, and every two weeks a nutrient solution (2.5 grams/liter of 20-19-18) was applied. Seedlings were measured and photographed on April 1, 1982.

STATISTICS. Statistical inferences from seed weights, germination, and comparative seedling heights are based on the nonparametric Wilcoxon rank-sum test (Lehmann, 1975).

RESULTS

CONES AND SEEDS. There were no significant differences between grove trees and isolated trees in cone length, cone weight, or number of seeds per cone

TABLE 1. **Comparison of cone and seed characteristics of isolated Metasequoia trees and those in mixed-clone groves.**

TREE NO.	LOCATION	MEAN CONE DIMENSIONS				MEAN NUMBER OF SEEDS				GERMINATION PERCENT	R*
		Length (cm)	R*	*Weight* (g)	R*	*Per cone*	R*	*Per pound*	R*		
ISOLATED TREES											
1	New Brunswick, New Jersey	1.95	5	2.01	6	92	5	500,000	8	0.67	6
2	Princeton, New Jersey	1.92	6	1.93	7	88	7	1,400,000	9	0.33	7
3	Princeton, New Jersey	2.11	4	2.30	5	106	1	380,000	7	0.00	8.5
4	Princeton, New Jersey	1.90	7	2.48	4	76	8	350,000	6	0.00	8.5
	Mean	1.97		2.18		90		657,000		0.25	
	Rank sum		22		22		21		30†		30†
GROVE TREES											
5	Princeton, New Jersey	2.12	2.5	3.18	1	99	3	300,000	4	2.00	4
6	Princeton, New Jersey	1.60	8	1.90	8	74	9	280,000	3	3.70	3
7	Princeton, New Jersey	1.56	9	1.30	9	89	6	230,000	2	30.61	2
8	Locust Valley, New York	2.26	1	2.84	2.5	94	4	320,000	5	1.47	5
9	Locust Valley, New York	2.12	2.5	2.84	2.5	104	2	145,000	1	46.67	1
	Mean	1.93		2.41		92		255,000		16.89	
	Rank sum		23		23		24		10†		10†

*Rank order used in statistical analysis.

†$P < 0.01$.

TABLE 2. **Germination of Metasequoia seeds tested at different temperatures.**

TREE NO.	DAY	TEMPERATURE (°C) 15	20	15/25	20/30	20/35
5	9	0/16*	13/16	5/20	11/21	3/16
5	13	0/16	16/16	16/20	16/21	9/16
5	17	2/16	16/16	17/20	21/21	14/16
5	22	2/16	16/16	17/20	21/21	14/16
9	9	0/7	4/7	4/8	6/8	7/7
9	13	3/7	5/7	4/8	8/8	7/7
9	17	3/7	5/7	4/8	8/8	7/7
9	22	3/7	5/7	4/8	8/8	7/7

*Zero germinants of 16 seeds.

(TABLE 1). Differences in number of apparently filled seeds per pound and in percentage of these that germinated were highly significant ($P < 0.01$). Grove trees ranked 1 through 5 in both seed weight and germination percentage, with each tree holding identical ranks for both test criteria. The probability that all grove trees would surpass all isolated trees in either seed weight or germination percentage by pure chance is only 1 in 126.

Five grams of seed from the Alabama grove tree produced 155 apparently sound seeds, of which 112 germinated; 5 g from the isolated tree produced 13

TABLE 3. **Comparative heights of 13-week-old Metasequoia glyptostroboides seedlings from isolated specimens and trees in mixed-clone groves.**

TREE NO.	NO. OF SEEDLINGS	MEAN HEIGHT (cm)	RANK
ISOLATED TREES			
1	3*	9.0	9
2	10*	9.3	8
Rank sum			17†
GROVE TREES			
5	10	13.7	3
6	10	14.0	1.5
7	8	12.7	5
9	9	11.7	7
10‡	10	14.0	1.5
11‡	9	12.2	6
12‡	10	13.5	4
Rank sum			28†

*In addition to these 13 isolated-tree seedlings, six others are mentioned in the text: one from no. 1 and two from no. 2 (seven weeks older), and three from the Alabama isolated tree (four weeks younger; two dead).

†$P < 0.05$.

‡Trees 10, 11, and 12 are in a grove at Bailey Arboretum, Locust Valley, New York. Seeds were collected in December and were not included in the tests reported in TABLE 1.

FIGURE 1. Thirteen-week-old *Metasequoia* seedlings from grove tree no. 5 (right) and isolated tree no. 1 (left).

apparently sound seeds, of which only 3 germinated. The order of difference in seed fertility between isolated and grove trees was the same in the Alabama trees as it had been in the New York and New Jersey ones.

Tetrazolium- and germination-testing of seedlots nos. 5, 7, and 8 gave similar results. Positive tetrazolium stains for the three lots, in order, were 5 of 7, 5 of 5, and 21 of 21; germination results were 6 of 7, 6 of 6, and 22 of 22. None of the seeds that failed to germinate gave a positive tetrazolium stain.

Among the five germination environments tested, constant 15°C was poorest, while constant 20°C, 15°/25°C, 20°/30°C, and 20°/35°C were satisfactory (TABLE 2). Visual inspection of germinants on day 13 showed those at 20°C and 20°/30°C to be larger than those at 15°/25°C, which in turn were much larger than those at 15°C and 20°/35°C.

SEEDLINGS. During the growth period, 3 of 19 isolated-tree seedlings died. One Alabama seedling was unable to shed its seed coat, and another had twisted cotyledons and failed to grow; 1 from lot no. 1 died after insecticide application. During this same period, only 1 of 128 grove-tree seedlings died. The difference in mortality was significant ($\chi^2 = 14.66$, $P < 0.01$).

Differences in height between the surviving isolated-tree and grove-tree seedlings were significant (TABLE 3, FIGURE 1). In addition to being slower growing, 3 of the 4 surviving seedlings of lot no. 1 and the sole surviving Alabama isolated-tree seedling were pale green in color, with some leaves having incipient fall coloration and tending to shrivel early. One seedling of lot no. 1 appeared normal, and all 11 of lot no. 2 appeared normal in color and habit, although they grew more slowly than grove-tree seedlings.

DISCUSSION

It seems reasonable to assume that our isolated trees' lighter seed weights and lower yield of fertile seed—and their progeny's higher seedling mortality, slower growth, cotyledon defects, and pale coloration—are all due to inbreeding depression. Apparently lots nos. 3 and 4 carry the greatest genetic load (recessive lethal and sublethal genes), because none of their seeds germinated. Lots nos. 1 and 15 seem to occupy an intermediate position: they produced five and three seedlings, respectively, of which all but one showed abnormal coloration or defective cotyledons. Lot no. 2 seems to carry the least load.

Conifers differ in their ability to "self," with some species showing greatly reduced seed set and others producing few to many viable seeds (Wright, 1976). Closely related to *Metasequoia, Sequoia* exhibits large clonal differences in relative germination of selfs and outcrosses (Libby *et al.*, 1981). The same is true of *Pseudotsuga menziesii*: self-pollinated ovules of some clones fail to produce viable seeds due to abortion of embryos (Orr-Ewing, 1957). Apparently, variation in the amount of genetic load carried by different trees causes some to be incapable of producing fertile self-pollinated seeds but allows others to produce a few viable seeds and occasional trees to self quite well. The amount of genetic load necessary to cause varying percentages of self-sterility has been calculated by several researchers (Bramlett & Popham, 1971; Bishir & Pepper, 1977).

Some of the variation in seed fertility among grove trees may be due to position in the grove with respect to availability of pollen from other clones. *Metasequoia* pollen is wingless and tends to clump together (U.S.D.A., 1974), and with this in mind I reexamined the spatial relationship of the grove trees to one another. Trees nos. 5 and 6 are at the uphill, northwestern (upwind at pollination time in March) end of their grove, while no. 7 is downhill, downwind, and surrounded by tall specimens bearing large quantities of microsporangiate strobili. In addition, the lower portions of the crowns of trees nos. 5 and 6 are suppressed, and megasporangiate strobili are present only in the tops, where pollen must be blown upward to reach them. Tree no. 8 stands in the open about 20 m from no. 9 and others.

It is clear from the comparison of germination- and tetrazolium-testing that no seed treatment (such as stratification) would have effected germination. To obtain good germination of *Metasequoia* seeds, one must collect cones from trees located advantageously for cross-pollination, then clean the seeds effectively by air-blower or equivalent technique to remove all empty ones. At the beginning of our experiment, it was difficult to distinguish filled and empty seeds in the diaphanoscope, and we ran the blower at medium speeds until we were able to judge its efficiency in retrospect by germination results. We then shifted to tetrazolium testing to determine which blower speed to use in cleaning seeds for the germination-environment tests and for the germination vs. tetrazolium comparison, and the resultant effects on germination percentage are obvious.

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DEPARTMENT OF HORTICULTURE & FORESTRY, COOK COLLEGE
NEW JERSEY AGRICULTURAL EXPERIMENT STATION
NEW BRUNSWICK, NEW JERSEY 08903

ADDITIONS AND CHANGES IN THE NEOTROPICAL CONVOLVULACEAE—NOTES ON MERREMIA, OPERCULINA, AND TURBINA

D. F. Austin and G. W. Staples

Since 1978 we have been preparing the first portion of the family Convolvulaceae for *Flora Neotropica*. To date, we have examined 17 genera and about 120 species. During this study various nomenclatural changes and additions have been necessary (Austin & Staples, 1980, 1981; Staples & Austin, 1981); further work has revealed the need for additional changes, and several new taxa require comment.

Merremia Dennst. is represented in the New World by almost 30 species, and there are several others in the Old World. Division of this genus from both *Ipomoea* L. and *Operculina* Silva Manso has been debated for generations, but our own studies (Austin, 1979; Austin & Staples, 1980, 1981; Staples, 1979; Staples & Austin, 1981) have convinced us that they are best treated separately.

THE MERREMIA DIGITATA COMPLEX

On the basis of scant material (about ten sheets) available to him, O'Donell (1941) recognized three species of *Merremia, M. digitata* (Sprengel) H. Hallier, *M. contorquens* (Choisy) H. Hallier, and *M. ericoides* (Meisner) H. Hallier. Growth habit and the degree and nature of the pubescence were the criteria used to separate these taxa. During our investigations we have had the opportunity to examine a sample (106 sheets total) larger than O'Donell's, including several type specimens unavailable to him. We found that O'Donell's characters do not provide consistent differentiation between these three nominate species; pubescence, in particular, intergrades completely among them. These taxa all have linear-lanceolate bracts 1–5 mm long, and calyxes with unequal sepals having noticeably scarious margins—characteristics that distinguish this complex from other, similar Brazilian campo/cerrado merremias (*M. cissoides* (Lam.) H. Hallier and *M. flagellaris* (Choisy) O'Donell). We prefer to recognize these somewhat arbitrary units as varieties of *M. digitata*. These can be distinguished with the aid of the key presented below, which is followed by the synonymy and the necessary new combinations.

Key to Taxa of the Merremia digitata Complex

1. Plants erect; sepals and stems glandular.......... *Merremia digitata* var. *ericoides*.
1. Plants decumbent or trailing; sepals and stems stellate to glabrous.
    2. Leaves entire to lobed, if lobed the lobes over 1 cm wide.................... .... *Merremia digitata* var. *elongata*.

Journal of the Arnold Arboretum **64**: 483–489. July, 1983.

2. Leaves digitately lobed, the lobes less than 1 cm wide. .... *Merremia digitata* var. *digitata.*

Merremia digitata (Sprengel) H. Hallier, Bot. Jahrb. **16:** 552. 1893, var. **digitata**

Gerardia digitata Sprengel, Syst. Veg. **2:** 808. 1825. TYPE: Brazil, *Sellow s.n.* (holotype, B 13788, presumably destroyed, photos at F, GH).

Ipomoea albiflora Moric. Pl. Nouv. Am. 114. *t. 70.* 1838; Choisy in DC. Prodr. **9:** 352. 1845; Meisner in Martius, Fl. Brasil. **7:** 230. 1869. TYPE: Brazil, apud Igreja Velha, *Blanchet 3330* (G-DC, *n.v.*; isotype, F).

Ipomoea albiflora var. *stricta* Choisy in DC. Prodr. **9:** 352. 1845. TYPE: Brazil, Minas Gerais, Serro Frio, *Martius s.n.* (holotype, presumably at M, *n.v.*, photo at FAU).

Ipomoea albiflora var. *divergens* Choisy in DC. Prodr. **9:** 352. 1845. TYPE: Brazil, Minas Gerais, Formegas, *Martius s.n.* (holotype, presumably at M, *n.v.*, photo at FAU).

Ipomoea albiflora var. *cinerea* Meisner in Martius, Fl. Brasil. **7:** 231. 1869. TYPE: Brazil, Minas Gerais, Oct. [no year], *Riedel s.n.* (holotype, presumably at M, *n.v.*).

Merremia digitata var. **elongata** (Choisy) Austin & Staples, comb. nov.

Batatas tomentosa var. *elongata* Choisy in DC. Prodr. **9:** 337. 1845. TYPES: Brazil, Minas Gerais, *Martius 1282* (syntype, M); São Paulo, campis Sorocuba, *Lund s.n.* (syntype, presumably at M, *n.v.*).

Ipomoea contorquens Choisy in DC. Prodr. **9:** 385. 1845. TYPE: Brazil, Minas Gerais, Serra de Cacarsa, *Martius 1007* (holotype, M).

Ipomoea maragniensis Choisy in DC. Prodr. **9:** 351. 1845. TYPE: Brazil, Maranhão, in sepibus ad fluv Itapicuru, Maragniensis, May [no year], *Martius 80* (holotype, M).

Ipomoea contorquens var. *α vulgaris* Meisner in Martius, Fl. Brasil. **7:** 286. 1869. TYPE: Brazil, *Sellow s.n.* (holotype, M).

Ipomoea contorquens var. *β heterophylla* Meisner in Martius, Fl. Brasil. **7:** 286. 1869. TYPE: Brazil, São Paulo, in campis graminosis siccisque pr. Villa Franca et Ypanema, Mar.–Jun. [no year], *Riedel s.n.* (holotype, M, *n.v.*).

Ipomoea contorquens var. *γ simplicifolia* Meisner in Martius, Fl. Brasil. **7:** 286. 1869. TYPES: Brazil, Minas Gerais, in arenosis montium Serra Frio pr. Tejuco, *Martius 1282* (syntype, M); prope Caldas, *Pohl s.n.* (syntype, M, *n.v.*), *Lund s.n.* (syntype, M, *n.v.*); in campis inter São Paulo et Jundiahy, *Lund s.n.* (syntype, M, *n.v.*).

Merremia contorquens (Choisy) H. Hallier, Bot. Jahrb. **16:** 552. 1893.

Merremia digitata var. **ericoides** (Meisner) Austin & Staples, comb. et stat. nov.

Ipomoea ericoides Meisner in Martius, Fl. Brasil. **7:** 251. 1869. TYPE: Brazil, Goiás, prope São Felis ad Rio Trahitas, *Pohl s.n.* (isotype, F 874820).

Merremia ericoides (Meisner) H. Hallier, Bot. Jahrb. **16:** 552. 1893; O'Donell, Lilloa **6:** 505. 1941.

NEW TAXA OF MERREMIA

Merremia repens Austin & Staples, sp. nov.

Herba; ramuli repentes, leviter stellati, trichomatibus cum 2 vel 3 ramis. Laminae palmatae, foliola 3 ad 5, ovato-lanceolata, petiolulata, 40–77 mm longa, 16–29 mm lata, stellata vel glabra. Cymae 2- vel 3-floribus, leviter pubescentes; sepala inaequales, dua exteriora orbiculato-ovata, 9–11 mm longa, glabra; sepala interiora ovato-lanceolata, 12–18 mm longa; corolla infundibuliformis, 40–50 mm longa, glabra, rosea (vel alba?); filamenta inaequalia, ad 25 mm longa.

Herb; stems creeping or twining at tips, longitudinally striate, sparsely pubescent with simple trichomes and 2- or 3-branched stellate trichomes, reaching 2 m in length and 1.5–2 mm in diameter. Leaves palmately divided to base; petiole cylindrical, 13–30 mm long, striate, with sulcus on upper side, stellate-pubescent; petiolules 4–6 mm long, sulcate, pubescent like petiole; leaflets 3 to 5, entire, ovate-lanceolate, 40–77 by 16–29 mm, median one largest, sparsely stellate-pubescent to glabrous, nerves sunken above and prominent below, lower surface stellate-pubescent or with numerous round, blackish dots, the apex obtuse to acute, mucronulate, the base cuneate, decurrent on petiolule, the margin slightly revolute. Inflorescences axillary, 2- or 3-flowered cymes, sometimes with 2 secondary dichasia arising from same axil; rachis faintly striate, 55–65 mm long, exceeding petiole of subtending leaf, sparsely pubescent, at distal end bearing fleshy lobe or ring surrounding bases of 2 peduncles attached to it; peduncles 13–15 mm long, nearly glabrous, each terminating in pair of unequal bracts, with 1 attached higher than other; bracts scalelike, 1–2.5 mm long, with median ridge on outer surface, mucronate or terminating in fleshy spur, edges membranaceous; pedicels clavate, 17–22 mm long, smooth, glabrous except for few trichomes at level of bracts. Sepals entire, unequal, the outer 2 orbiculate-obovate, 9–11 by 6–7 mm, the inner 3 ovate-lanceolate, 12–18 by 7–8 mm, acute-attenuate at apex, truncate at base, glabrous, membranaceous; corolla funnelform, 40–50 by 30–35 mm, glabrous, rose-pink (or white); stamens unequal, 22–25 mm long, the filaments simple, glabrous, the anthers spirally dehiscent at anthesis, 5–7 mm long, the pollen smooth, 3-colpate; ovary not seen, the style simple, filiform, 20–21 mm long, the stigma 2 mm in diameter, 2-lobed, lobes globose. Fruits and seeds unknown.

TYPES: Brazil, Minas Gerais, Cerra do Cipó, km 135, 19 Feb. 1980, *H. S. Irwin et al. 20526* (holotype, NY); Serra do Espinhaço, lower slopes of Pico de Itacolomi, S of Ouro Prêto, 1600 m, 30 Jan. 1971, *H. S. Irwin et al. 29376* (paratypes, FAU, NY).

There is some question concerning the flower color of this taxon. The label on the holotype collection clearly states "rose-pink," and this color is visible on the buds (there are no open flowers on the type). The paratypes are morphologically similar to the holotype, but the label information indicates that the corollas are white. While it is possible (given the variability in corolla color within the family) for this species to have both pink and white flowers, such a condition has not previously been observed in *Merremia.*

Corollas that are any shade of red are extremely uncommon in *Merremia*; *M. weberbaueri* Ooststr. of Peru is the only species of the genus known to have them. Although superficially similar to *M. repens, M. weberbaueri* has incompletely palmatifid leaves, is completely glabrous, has flowers to 7.5 cm long, and is known only from the western side of the Andes in Peru. Despite the large disjunction in their ranges, it seems likely (based on their morphology) that the two species are closely related. Since neither is well represented in North American herbaria (we have seen a total of about ten sheets for both) and the region between their known ranges has not been well collected, it is possible that they are not as widely geographically separated as it seems.

Within the area where *Merremia repens* has been found, two other species of *Merremia* occur that may be confused with it. *Merremia macrocalyx* is an extensive liana that is either completely glabrous or sparsely pubescent with simple trichomes and generally has numerous (up to 20) flowers in compound cymes. *Merremia digitata* has palmately divided leaves; plants of this species are much smaller in both vegetative (leaflets 20–40 mm long) and floral (corolla 28–33 mm long) dimensions and are generally much more pubescent than those of *M. repens.*

Merremia species A

Based on the very fragmentary material available to date, this appears to be an undescribed species of *Merremia.* Although it shares features with several other species of that genus, the taxon has an apparently unique combination of leaf shape and surface characters, as noted below. Until we are able to examine more material, we prefer not to propose a specific epithet. We give the information here to alert herbarium curators and collectors to the need for more specimens.

Herb; stems twining(?), cylindrical, striate, sparsely stellate-pubescent to glabrous, 1 mm in diameter. Leaves palmately divided to base; leaflets 5, petiolulate, ovate-lanceolate, nerves sunken above, the upper surface glabrous, dark brown-black when dry, the lower surface whitish stellate-tomentose, the apex obtuse to acute, the base acute. Sepals unequal in bud, glabrous, the outer 2 covering the inner 3; anthers (undehisced) 10–12 mm long, the pollen 3-colpate, nonspinulose. Corolla, fruit, and seeds not seen.

If one judges by the general aspect of the fragments, this taxon most resembles *Merremia platyphylla* (Fern.) O'Donell of southwestern Mexico. The length of the anthers, in particular, suggests this species, which has the longest anthers of any species of *Merremia* we have seen. Specimens of *M. platyphylla* that we have examined are completely glabrous or have sparse, simple trichomes markedly distinct from the stellate indumentum of species A. In pubescence type, occurrence of trichomes only on the lower surface of the leaflets, and coloration of dried material, this species matches *Merremia nervosa* Pittier, a Venezuelan endemic. The latter is only known to have trifoliolate leaves, however.

Geographic ranges of *Merremia platyphylla* and *M. nervosa* do not correspond to that of species A. Printed labels attached to the two fragments from the Field Museum indicate Peru or Chile as the origin of the material; neither of the similar taxa occurs in this region, as noted above. Collection localities published in *Plantae Novae Hispaniae* (Sessé & Moçiño, 1887) are vague; *Convolvulus pentaphyllus,* to which these fragments had been referred, is cited

(p. 23) from "caliodore America." Many of the other species of Convolvulaceae listed in *Plantae Novae Hispaniae* are found in Mexico; we believe that these fragments might have originated in Mexico also, and that they may represent an undescribed form of *M. platyphylla* or a species related to it. Additional, complete specimens are needed to ascertain the status of this taxon.

Fragments examined (*Sessé, Moçiño, Castillo, & Maldonado 890* and *5022*, both F, accessioned as 844986 and 846511) are labeled "Novae Hispaniae, in vice-regno Chilii et Peruvii lectae," without date.

OPERCULINA

Operculina is a small genus with less than 12 taxa in the New World; several others occur in the Old World. During our study we have found a need for a name change for the most common American species, and an atypical variant of that species.

Operculina hamiltonii (G. Don) Austin & Staples, comb. nov.

Ipomoea hamiltoni G. Don, Gen. Syst. **4:** 268. 1838. This is a new name for *Convolvulus alatus* Ham. Prodr. Fl. Ind. Occ. 24. 1824, not *C. alatus* (R. Br.) Sprengel, 1819.
Convolvulus alatus Ham. Prodr. Fl. Ind. Occ. 24. 1824. TYPE: Tobago, Scarborough, *Hamilton s.n.* (not found).
Ipomoea alulata Miq. Linnaea **18:** 599. 1844. TYPE. Surinam, crecit prope Paramaribo, *Miquel s.n.* (lectotype, U).
Ipomoea altissima Martius ex Choisy in DC. Prodr. **9:** 359. 1845; Meisner in Martius, Fl. Brasil. **7:** 213. 1869. TYPE: Brazil, Amazonas, Rio Negro, *Martius s.n.* (syntype, M, photo at NY).
Ipomoea ampliata Choisy in DC. Prodr. **9:** 361. 1845. TYPE: Mexico, "in Campeche, in oceani Pacifici" (syntype, BM, *n.v.*).
Operculina altissima (Martius ex Choisy) Meisner in Martius, Fl. Brasil. **7:** 213. 1869.
Ipomoea pterodes Choisy in DC. Prodr. **9:** 361. 1845. TYPE: French Guiana, Cayenne, *Gabriel s.n.* (holotype, G-DC).
Operculina pterodes (Choisy) Meisner in Martius, Fl. Brasil. **7:** 213. 1869.
Operculina pterodes f. *pubescens* Pilger, Bot. Jahrb. **30:** 186. 1901. TYPE: Brazil, Mato Grosso, Bandeira bei Cuiabá, *H. Meyer 325* (holotype, B, presumably destroyed; no duplicates found).
Operculina alata (Ham.) Urban, Symb. Antill. **3:** 343. 1902; Powell, Jour. Arnold Arb. **60:** 244. 1979; Austin & Staples, Mem. New York Bot. Gard. **32:** 322. 1981.
Operculina alata var. *pubescens* (Pilger) O'Donell, Lilloa **30:** 61. 1960.

The name *Operculina alata* (Ham.) Urban has predominated in the literature since the combination was made in 1902 (see Powell, 1979; Howard *et al.*, 1981; Austin & Staples, 1981). No one seems to have noted that G. Don (1838) was correct in stating that *Convolvulus alatus* Ham. is a later homonym and that, as such, the specific epithet published by Hamilton is unavailable. We therefore propose the new combination *Operculina hamiltonii,* using the next available name.

We have examined about 200 collections of *Operculina hamiltonii,* as well as a number of living plants in several countries in the northern part of its range. While there is considerable variation within the species, one collection from the southern part of the range appears to us to fall beyond that noted elsewhere. The leaves are markedly mucronate and the sepals smaller; these traits do not appear to this extreme in the northern part of the range. We believe the difference sufficient to merit varietal status.

Operculina hamiltonii var. **mucronata** Austin & Staples, var. nov.

Ad varietatem hamiltonii similis, sed foliis angustiis lanceolatisque mucronatis, sepalis obovatis minoribus (16–18 mm vs. 25–30 mm) divergens.

Herb; stems prostrate or perhaps twining at tips, cylindrical, to 2 mm in diameter, striate to sub-alate. Leaves with petiole stout, 5–12 mm long, striate, sulcate; blade entire, lanceolate-hastate, 74–87 by 7–14 mm, the nerves impressed above and prominent below, the apex attenuate, mucro to 1 mm long, the base cordate to auriculate, the margin slightly revolute. Flowers axillary, solitary; peduncle slender, 50–70 mm long, striate basally to alate distally, or striate throughout; bracts 2, membranaceous, attenuate-deltoid, 5–9 by 1–2 mm, apically attenuate, basally truncate, probably caducous; pedicel thickened, clavate, 9–15 by 3–4 mm, striate to 5-angled; calyx pyriform, reddish brown when dried, the sepals entire, obovate, ± equal, 16–18 by 7–8 mm, acute and mucronate at apex, truncate at base, margin membranaceous; corolla campanulate, 36–38 by 38–43 mm, yellow, sericeous on tips of interplicae, otherwise glabrous; stamens unequal, included, the filaments filiform, the anthers spirally dehiscent, 3–4 mm long. Fruits unknown.

TYPE: Brazil, Mato Grosso, Serra das Araras, in campo aprico, 14 Feb. 1894, *Lindman A2997* (2 sheets) (both S; holotype numbered 1 and isotype numbered 2 on our annotation labels).

TURBINA

Five species of *Turbina* are known in Neotropical regions; several others occur in Paleotropical areas. For many years there has been confusion and difficulty in separating this genus from *Ipomoea*. The indehiscent, usually one-seeded fruits of *Turbina* are distinctive. Since *Flora Brasiliensis* was published in 1869, the following species of *Turbina* has been misidentified as an *Ipomoea*. Only upon examination of fruiting material did we notice the difference.

Turbina cordata (Choisy) Austin & Staples, comb. nov.

Rivea cordata Choisy in DC. Prodr. **9:** 326. 1845. TYPES: Brazil, Minas Gerais, in sylvis catingas ad fluv. St. Francisco prope Salgado, *Martius s.n.* (lectotype, G-DC; isolectotype, M, *n.v.*, photo at FAU); *Pohl s.n.* (syntype, M, *n.v.*, photo at FAU).

Ipomoea martii Meisner in Martius, Fl. Brasil. **7:** 258. 1869. A substitute name for *Rivea cordata.*

There are three taxa in South America that have been confused and misidentified by Choisy, Meisner, and others. Choisy also misidentified a fourth species. Thus *Ipomoea tubata* Nees (Brazil), *I. subincana* Choisy (Brazil), *Turbina abutiloides* (H.B.K.) O'Donell (Ecuador to Venezuela and Panama), and

T. cordata (Choisy) Austin & Staples (Brazil) have all been misidentified. The two species of *Ipomoea* are typical members of sect. ERIOSPERMUM Hallier f., having dehiscent, two- to four-valved fruits and seeds with long, woolly trichomes along the margins.

When Choisy named *Rivea cordata*, he included specimens of *Ipomoea tubata* but not the type of that species. Thus, Choisy's concept of *Rivea cordata* included two taxa, one of which may be assigned to *I. tubata* Nees as per the Code. That makes his binomial applicable to remaining specimens. Instead of transferring the epithet to *Ipomoea*, however, Meisner (1869) created the substitute name *I. martii*. To bring the names in line with modern nomenclature, we have used the earliest specific epithet for the taxon.

Since a complete description of both *Turbina abutiloides* and *T. cordata* will be published with a key to the genus in *Flora Neotropica*, we will not give a detailed discussion here.

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D. F. A.
DEPARTMENT OF BIOLOGICAL SCIENCES
FLORIDA ATLANTIC UNIVERSITY
BOCA RATON, FLORIDA 33431

G. W. S.
HARVARD UNIVERSITY HERBARIA
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

JOURNAL OF THE ARNOLD ARBORETUM
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STUDIES IN THE CRUCIFERAE OF WESTERN NORTH AMERICA

REED C. ROLLINS

SIGNIFICANT NEW TAXA of the family Cruciferae keep surfacing as a result of the search for rare and endangered species. This work, under the auspices of various federal government agencies and state natural heritage programs, is accompanied by the renewed interest of both amateurs and professionals in the native flora and fauna. In the western United States participants are getting into areas never before explored by botanists, and some of the resulting discoveries are spectacular (Rollins, 1982). Although the western United States is one of the principal centers of diversity for the Cruciferae and the area might therefore be expected to yield an occasional taxon never before seen, the number being brought to light is almost an embarrassment considering that I have been pursuing systematic studies on this family for more than 45 years.

Of even greater interest than their newness, however, is the fact that some of these new taxa form the basis for an understanding of evolutionary pathways heretofore not fully grasped. For example, the silique morphology of *Physaria obcordata* Rollins, a new species described below, helps to explain how species of *Physaria* (Nutt.) A. Gray have evolved an added mode of seed dispersal entirely different from that of their putative evolutionary progenitors in *Lesquerella* S. Watson.

It has generally been agreed (Payson, 1922; Rollins, 1939, 1950; Maguire & Holmgren, 1951; Mulligan, 1968; Rollins & Shaw, 1973) that *Physaria* is very closely related to *Lesquerella* and was probably derived from it evolutionarily. Of these two genera, *Lesquerella* contains the more primitive species; therefore, identifiable trends away from features characteristically present in that genus would represent evolutionary changes—perhaps toward superior fitness for survival.

The efficiency of seed dispersal is something that can be examined in this connection. In *Lesquerella* the valves of the siliques dehisce and fall away, leaving the seeds to fall more or less independently. Thus, the seeds are freed from the siliques to be dispersed by whatever agent is operative. In the region

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where *Lesquerella* abounds, wind and water are (aside from gravity) perhaps the most important dispersing agents for seeds of the type produced by *Lesquerella* and *Physaria*.

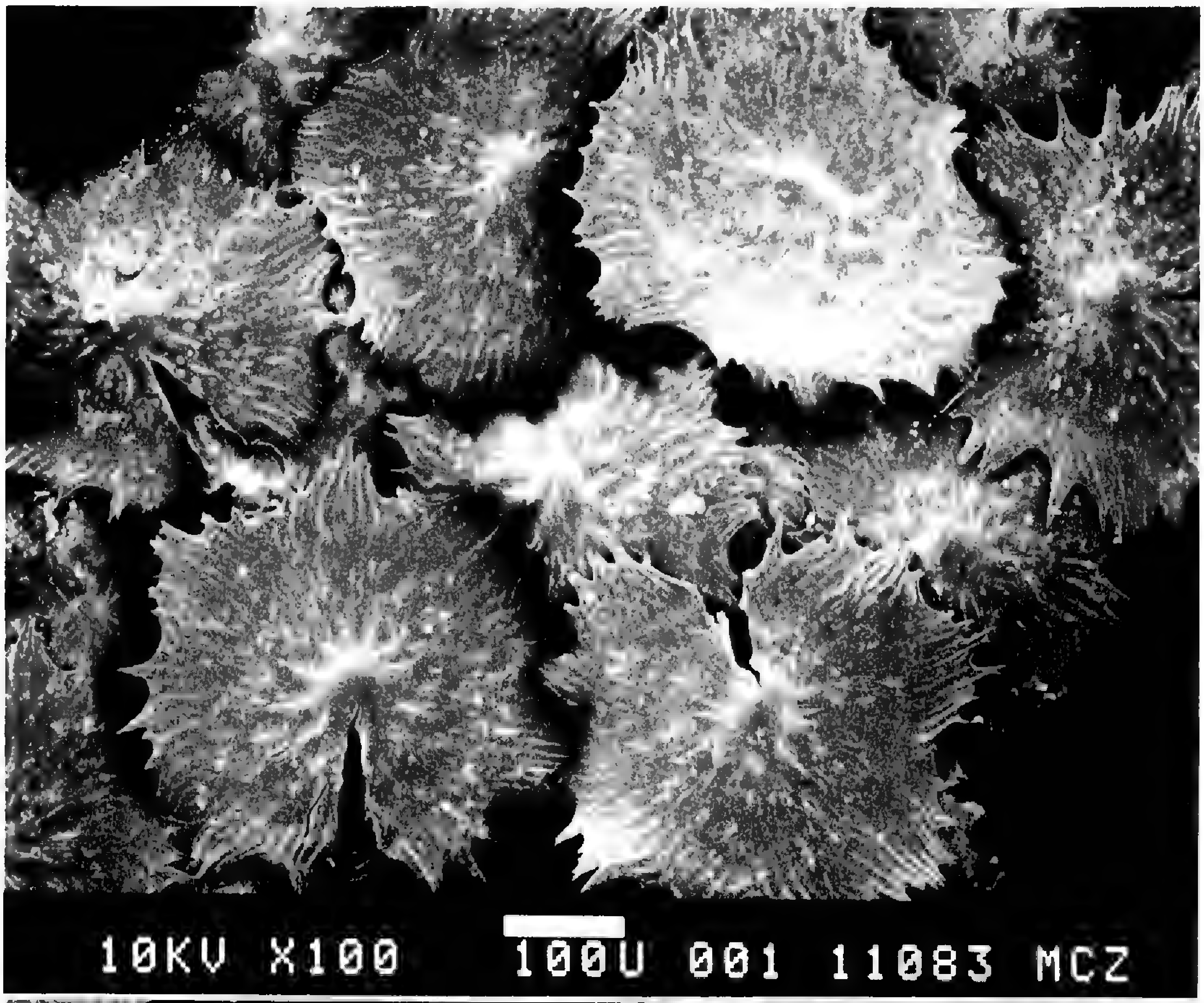
Although wind is a very important dispersing agent for many species in the more arid parts of western North America, none of the many species of *Lesquerella* in this region (Rollins & Shaw, 1973) has evolved a mechanism to take advantage of wind dispersal. The seeds are not winged in the more westerly species, although they are narrowly winged or margined in some from the more easterly range of the genus (Texas to Alabama and Tennessee). The siliques of *Lesquerella* are in no way modified for wind dispersal. In *Physaria*, however, the siliques show an evolutionary line from a situation similar to that of *Lesquerella* to one in which the silique valve has become modified so that the valve, enclosing one or more seeds, is the unit of dispersal rather than the seed itself. With narrowing of the replum and constriction of the valves, the seeds become entrapped and can go only where the valves take them. The inflated valves become highly mobile after dehiscence and are moved by even mild wind currents.

Of the several evolutionary trends recognizable in *Physaria*, two are easily associated with dispersal. The first is a trend from minimum lateral constriction of the valves at the replum with no entrapment of the seeds, as found in *P. obcordata* and *P. geyeri* (Hooker) A. Gray, to a situation of maximum lateral constriction of the valves at the replum and a complete entrapment of the seeds within, as in *P. acutifolia* Rydb., *P. chambersii* Rollins, *P. floribunda* Rydb., and several other species. In the most extreme cases the orifices of the valves are so narrow that seeds are not spilled out as the valves are tumbled along by the wind. This ensures movement of the seeds away from the parent plant—in many instances for a considerable distance. The second trend is from scarcely inflated valves (as shown by *P. geyeri*) through modestly inflated (as in *P. obcordata*) to highly inflated ones (as in *P. chambersii, P. lepidota* Rollins, *P. newberryi* A. Gray, and several other species). In addition, more or less indurated valves tend to be uninflated, while papery ones are highly inflated. This can be seen between and even within species: for example, some populations of *P. acutifolia* and *P. alpestris* Suksdorf have siliques with only slightly inflated, indurated valves, while others have siliques with thinner, highly inflated ones. Over most of the geographic range of the species, populations of *P. didymocarpa* (Hooker) A. Gray have siliques with heavy-walled valves, but var. *integrifolia* Rollins, which is restricted to western Wyoming and eastern Idaho, has thin, highly inflated valves. In each of these cases, the thin, inflated silique valves are better adapted for wind dispersal than the heavier-walled, less inflated ones.

The implications of the development of a wholly different dispersal mechanism in *Physaria* not only are evolutional but also involve adaptation to the environment. Advantages might accrue to *Physaria* for either competition or long-term survival. Any such advantages are in addition to the seed-dispersal features of *Lesquerella* species of the same region, since the seeds of *Physaria* and *Lesquerella* in this area are very similar.

Three observations must be considered in determining whether or not *Physaria* has effective dispersal advantages over *Lesquerella*. First, in areas where both genera occur, *Physaria* is generally by far the more aggressive colonizer. Plants of *Physaria* readily invade the talus of road-cuts and embankments and are usually more abundant than *Lesquerella* in disturbed sites of this type throughout the Rocky Mountain and Intermountain regions (Rollins, 1981). Second, there is no substantial difference in the total distribution in the region of species of the two genera. Some species of *Physaria* have a relatively wide geographic range (for example, *P. didymocarpa*, Alberta to Wyoming; *P. acutifolia*, Idaho and Wyoming to New Mexico), while others are restricted in range (e.g., *P. lepidota*, south-central Utah; *P. condensata* Rollins, southwestern Wyoming; *P. oregona* S. Watson, Snake River drainage on the border of Oregon and Idaho). Similarly, *Lesquerella* of the Cordilleran region has widespread species, such as *L. alpina* (Nutt.) S. Watson (Alberta and Saskatchewan to Colorado and Utah) and *L. kingii* S. Watson (Idaho and Utah to California), and others with a restricted distribution, such as *L. garrettii* Rydb. (Wasatch Mountains of Utah), *L. macrocarpa* A. Nelson (south-central Wyoming), and *L. cinerea* S. Watson (north-central Arizona). Third, the fact that the seeds of *Physaria* are more readily dispersed than those of *Lesquerella* may compensate to some extent for the longevity of individual plants of *Physaria*. Observations on a plant of *P. floribunda* in Colorado showed nine successive separated positions of leaf scars from basal leaves on the enlarged caudex. This plant was at least ten years old. Individuals of most species of *Physaria* show evidence of considerable age—quite in contrast to most of the perennial species of *Lesquerella*, which tend to be short lived. Having a mechanism that moves the seeds out of the competitive range of a mother plant that is going to remain in position for many years is a distinct advantage. Otherwise the seeds are dropped nearby, and unless they are washed away the resulting young seedlings would be in direct competition with the mother plant, having an ultimate deleterious effect on the reproductive capacity of the population as a whole. Both the number of viable seeds produced and where they end up with respect to the existing plants affect a given population in size and structure.

From the above field observations on *Physaria* and *Lesquerella*, it can be concluded that the development of an entirely new seed-dispersal mechanism has not provided *Physaria* species with significant increases in geographic distribution over *Lesquerella* species of the same general region. However, it has provided the basis for aggressive colonization of disturbed habitats and has probably increased the number of individuals in many species to the point where *Physaria* is one of the most frequently seen crucifers (other than weeds) along road-cuts and fills at middle and lower elevations in the mountains of the Rocky Mountain and Intermountain states. Having an added mechanism to ensure the movement of seeds away from the mother plant counteracts to some extent the disadvantages of long-lived plants in a rapid buildup of populations in favorable sites. The long-term effect should be to keep the gene pools of populations of *Physaria* well dispersed and to provide the basis for quick utilization of new environmental conditions as they arise.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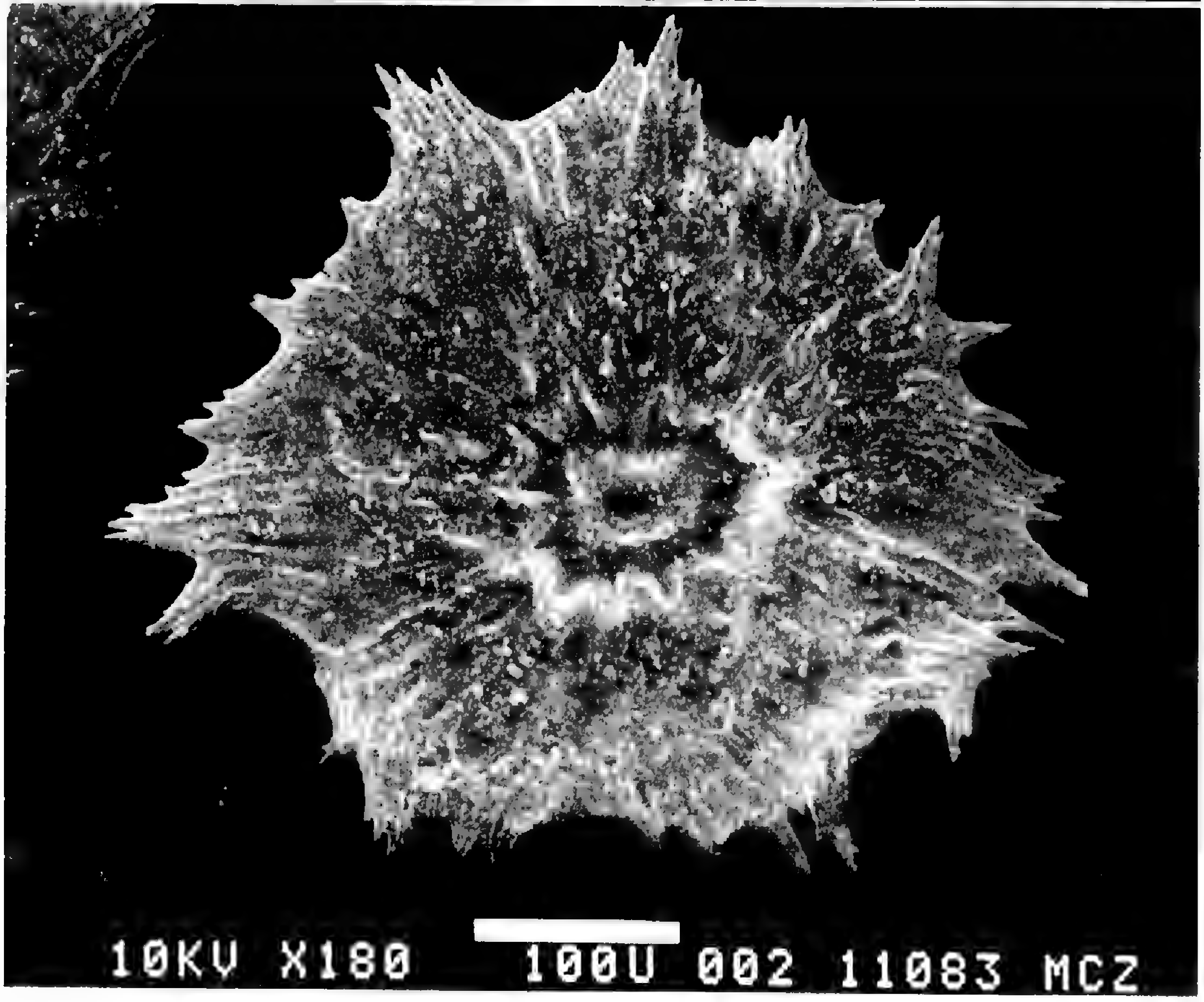
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Physaria obcordata Rollins, sp. nov. FIGURE 1.

Herba perennis; caudicibus crassis ramosis; foliis radicalibus petiolatis, late oblanceolatis, integris vel parce sinuatis, acutis, lepidotis, argenteis, 4–8 cm longis, 1–1.5 cm latis; foliis caulinis anguste lanceolatis, integris; caulibus erectis vel decumbentibus, 12–18 cm longis; pedicellis fructiferis late divaricatis vel recurvatis, 1–1.5 cm longis; siliquis didymis, parce inflatis, obcordiformibus; loculis 2-ovulatis; replo late obovato vel prope orbiculari; stylo 3–5 mm longo; seminibus immarginatis suborbicularibus; cotyledonibus accumbentibus.

TYPE. Colorado, Rio Blanco Co., T2S, R97W, S9, USGS Square S Ranch Quadrangle, ca. ¼ mi NE of junction of Hog Lot Draw and Piceance Creek, on shale of Green River Formation, 1890 m alt., 8 July 1982, *W. Baker & T. Naumann 82-277* (holotype, GH).

Perennial with deep, thickened root; thick branches of caudex invested with old overlapping leaf-bases; leaves, stems, pedicels, and siliques densely covered with minute lepidote trichomes with numerous rays fused to their tips. Basal leaves numerous, erect rather than rosulate, petiolate, 4–8 by 1–1.5 cm; blade broadly oblanceolate, acute, entire to sparingly sinuate-dentate, silvery. Fertile stems arising among basal leaves, simple, erect to decumbent, 12–18 cm long. Cauline leaves narrowly lanceolate, lower ones petiolate, upper ones cuneate at base. Flowering pedicels divaricately ascending, straight; sepals oblong, non-saccate, 4–5 by ca. 2 mm, densely pubescent; petals erect, spatulate, gradually narrowed from widest place to point of insertion, not differentiated into blade and claw, 7–9 by ca. 3 mm, yellow; filaments not expanded, the anthers sagittate, ca. 2 mm long. Infructescences elongated, occupying nearly one-half length of stems, congested; pedicels widely spreading to recurved, 1–1.5 cm long; siliques usually pendent, obcordate with deep open sinus, to nearly truncate above and with no sinus below, usually slightly inflated, the valves uneven in outline, usually with high shoulder above sinus, the replum broadly obovate to nearly orbicular, 4–5 by 3–5 mm, entire, the funiculi 2 (rarely 3 or 4) per loculus, near apex of replum, attached to septum from near middle toward base. Seeds nearly orbicular to broadly oblong, plump, wingless, 2.5–3.5 mm in diameter; radicle equaling or shorter than cotyledons; cotyledons accumbent.

SPECIMENS EXAMINED. **Colorado.** RIO BLANCO CO.: T2S, R97W, S9, USGS Square S Ranch Quadrangle, scattered on Green River Formation, ca. ¼ mi NE of junction of Hog Lot Draw and Piceance Creek, 1890 m alt., *Baker & Naumann 82-209* (CS, GH); T1N, R100W, S1, USGS Calamity Ridge Quadrangle, 0.4 mi WSW of Greasewood Mtn., 2170 m alt., *J. Walker & Riefler 82-361* (CS, GH); T1N, R100W, S1, USGS Calamity Ridge Quadrangle, 1.9 mi WNW of Caldwell Camp, 2158 m alt., *Walker & Riefler 82-363* (CS, GH); T2S, R97W, S4, USGS Square S Ranch Quadrangle, North Dudley Creek, ca. ¾ mi NE of junction of North Dudley and Piceance creeks, 1950 m alt., *Baker & Naumann 82-193* (CS, GH).

FIGURE 1. SEM photos of trichomes of **Physaria obcordata** (*Walker & Riefler 82-361*): above, overlapping layers on leaf surface (split in some trichomes an artifact produced during preparation of sample); below, single trichome showing extensive webbing between rays (point of attachment to leaf on opposite side, near center).

The epithet *obcordata* refers to the shape of the silique. The minute, scalelike trichomes and the upright basal leaves with stems arising largely within the leaf-cluster that characterize *Physaria obcordata* suggest a close relationship to *P. lepidota,* which shares these features. The latter is the only other known species of the genus that has even nearly similar trichomes. The two species resemble each other in growth habit and other characters, but their siliques are entirely different. Those of *P. lepidota* are highly inflated with deep sinuses above and below; in age, they are erect on straight or nearly straight, divaricately ascending pedicels. Those of *P. obcordata* are only slightly (if at all) inflated, with an open sinus above that varies in depth but with no sinus below; in age, they are usually pendent on recurved pedicels. Actually, the siliques of *P. obcordata* are more similar to those of *P. geyeri* (although they are less compressed than in that species) than to those of any other known species of *Physaria.* This is reflected in the shape of the replum: in *P. obcordata* it is broader, ranging from broadly obovate to nearly orbicular with a rounded apical area, while in *P. geyeri* it is narrower, ovate, and with an acute apical area. Both species usually have two ovules in each loculus, although *P. obcordata* occasionally has three or four.

The discovery of *Physaria obcordata,* which combines the silique shape and reduced ovule number characteristic of *P. geyeri* with the habit and trichome type of *P. lepidota,* strengthens the argument for keeping *P. geyeri* in *Physaria* (Rollins & Shaw, 1973) and not considering it to be a species of *Lesquerella* as was done by Mulligan (1968).

I was recently surprised to discover in a *Physaria* trichomes with numerous rays embedded in a matrix extending nearly to the ray tips (Rollins, 1981). This trichome type, while well known in the related genus *Lesquerella,* had not been seen in any species of *Physaria* until *P. lepidota* was discovered. It is quite remarkable that within two years of that discovery, another species with even more extreme trichome webbing has been found. In the trichomes of *P. obcordata,* the matrix cementing the rays together extends to the very ends of the ray tips (see FIGURE 1). These trichomes are peltate and occur in many overlapping layers, completely encrusting the surfaces of the leaves. These trichomes can be compared with those of *P. lepidota* by examining previously published SEM pictures (Rollins, 1981).

NEW TAXA OF ARABIS, DESCURAINIA, DRABA, LESQUERELLA, AND POLYCTENIUM

Arabis tiehmii Rollins, sp. nov. FIGURE 2.

Herba perennis; caudicibus crassis; foliis radicalibus erectis, spathulatis vel oblanceolatis, prope glabris, acutis, 1.5–2.5 cm longis, 4–6 mm latis; foliis caulinis 3–5, glabris, oblongis, sessilibus, 8–12 mm longis; caulibus tenuibus, glabris, 8–17 cm altis; pedicellis tenuibus, erectis vel divaricatis, rectis, 3–5 mm longis; siliquis glabris acutis 16–22 mm longis, 1.5–2 mm latis; seminibus oblongis, ca. 2 mm longis, ca. 1 mm latis; cotyledonibus accumbentibus.

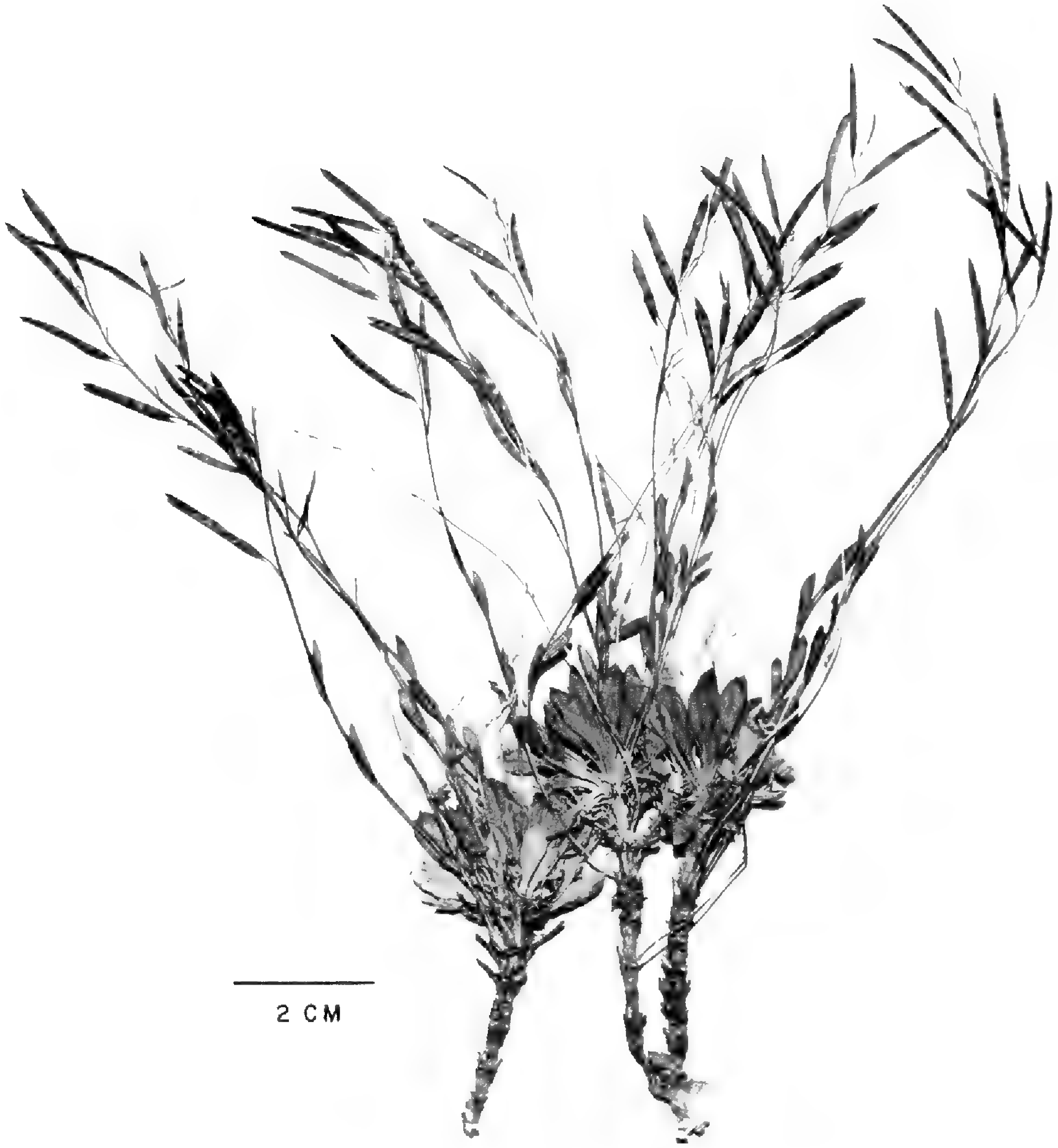

FIGURE 2. **Arabis tiehmii** (*Tiehm 7561*), showing elongated, thickened caudex with old leaf-bases.

TYPE. Nevada, Washoe Co., Sierra Nevada, Carson Range, ridge N of Mt. Rose, ¾ air mi NNW of peak, near rock outcrops on decomposed granite, 19 Aug. 1982, *A. Tiehm 7561* (holotype, GH; isotypes to be distributed).

Perennial; caudex simple or closely branched, thickened with old leaf-bases. Basal leaves tufted, erect, petiolate, 1.5–2.5 cm by 4–6 mm; blade spatulate to oblanceolate, acute and often apiculate with large simple trichome, entire, grayish green, 1-nerved from base to apex, glabrous except for marginal forked or simple trichomes on petiole margins. Cauline leaves 3 to 5, sessile, oblong, 8–12 mm long, acute, the lower ones cuneate at base, glabrous or with occasional trichomes along margin toward base, the upper ones cuneate at base or sometimes with minute auricles. Stems slender, erect to somewhat decumbent, often flexuose, 8–17 cm long, glabrous. Fruiting pedicels straight, divaricately ascending to erect, slender, 3–5 mm long, glabrous; siliques erect to slightly divaricate, flattened parallel to septum, 16–22 by 1.5–2 mm, acute, glabrous, 1-nerved below; style barely evident to less than 0.5 mm long. Seeds oblong, plump, wingless on sides but with abbreviated wing distally, ca. 2 by 1 mm; cotyledons accumbent.

In growth habit, *Arabis tiehmii* is more similar to *A. davidsonii* E. Greene than it is to any other species of *Arabis* L. The caudex is similarly thickened with old leaf-bases but is not nearly as heavy as in that species (see FIGURE 2). In such characters as the tufted basal leaves, thickened caudices, flexuose stems, and ascending siliques, *A. tiehmii* is much like *Smelowskia holmgrenii* Rollins. This resemblance prompted me to examine *S. holmgrenii* again, with the thought that it might be better placed in *Arabis* than in *Smelowskia* C. A. Meyer. The nearly terete siliques, incumbent cotyledons, and unguiculate petals, however, preclude it from the genus *Arabis.* Since these are features of *Smelowskia,* it seems best to leave *S. holmgrenii* in *Smelowskia* even though it is clearly not closely related to other known species of the genus.

In a comparison of *Arabis tiehmii* and *A. davidsonii,* differences in the length of the siliques, the length of the basal leaves, and the nature of the seeds stand out. Both the siliques and the basal leaves of *A. davidsonii* are more than twice as long as those of *A. tiehmii.* Also, the petiole of the basal leaves of *A. davidsonii* is long, while that of *A. tiehmii* is scarcely defined, with the blades merely tapering to the point of insertion. The seeds of *A. tiehmii* are narrowly oblong, with an abbreviated thickish wing only at the distal end; those of *A. davidsonii* are broadly oblong to orbicular and narrowly winged all around.

Arabis davidsonii was at one time confused with *A. lyallii* S. Watson and was even made a variety of it by Smiley (1921). However, neither *A. davidsonii* nor *A. tiehmii* is considered to be closely related to *A. lyallii.* Now that there are two known species having much-thickened caudices with numerous leaf-bases (see FIGURE 2) (vs. the relatively slender, nearly naked caudex branches of *A. lyallii*), it is easy to see the evolutionary trend that resulted in these distinctive structures. With *A. tiehmii* as a near relative, *A. davidsonii* is no longer a somewhat anomalous species in the genus *Arabis.*

J. W. Congdon C10 (GH) is a fragmentary specimen, consisting of one fertile stem, a separate infructescence, and a few basal leaves, which I previously referred doubtfully to *Arabis davidsonii.* It was collected at Mt. Warren Pass, Mono Co., California, on 21 August 1894. The siliques are short like those of *A. tiehmii,* and the seeds are oblong with more of a wing. I believe this specimen is closer to *A. tiehmii* than to *A. davidsonii,* but there is still room for doubt because of the inadequacy of the material.

Arabis rigidissima Rollins var. **demota** Rollins, var. nov.

Herba perennis; siliquis valde 1-nervatis, obtusis, 4–6 cm longis, ca. 3 mm latis; seminibus late oblongis vel prope orbicularibus, alatis.

TYPE. Nevada, Washoe Co., Sierra Nevada, Carson Range, Galena Creek, T17W, R19E, S17, 1.5 air mi ESE of Mt. Rose peak, 7900 ft alt., rocky areas at the edge of aspen groves, 26 Aug. 1982, *A. Tiehm 7572* (holotype, GH; isotypes to be distributed).

Stems one or few from branched or simple, ligneous or subligneous base, usually branched, stiff, with branches rigidly ascending. Leaves narrowly petiolate; blade oblanceolate, pubescent with 3 or 4 branched dendritic trichomes, tufted. Pedicels and siliques divaricately ascending, glabrous; siliques few, remote, straight to slightly curved, 4–6 cm by ca. 3 mm, obtuse at apex, the valves veiny, strongly 1-nerved nearly to apex, margins slightly uneven, the style absent or very short. Seeds in single row, flattened, winged, broadly oblong to nearly orbicular, 2.5–3 mm long or in diameter, wing ca. 0.5 mm wide; cotyledons accumbent.

True *Arabis rigidissima* has only rarely been collected, and to my knowledge it is restricted to Trinity and Humboldt counties in California, 200 or more miles northwest of the site where var. *demota* was found. The differences between var. *rigidissima* and var. *demota* are minor but consistent and show that the populations have diverged evolutionarily enough to merit nomenclatural recognition. In var. *rigidissima* there is a definite style present and the siliques are acuminate toward the apex, while in var. *demota* there is no style or only the barest suggestion of one and the silique apex is obtuse or at most acute. In var. *demota* the valves are prominently veined and a strong nerve beginning at the base reaches to near the tip, while in var. *rigidissima* the valves hardly show any veininess and the much-less-distinct nerve reaches only just above the middle. The seeds of var. *rigidissima* are more nearly orbicular, and the winging surrounds the entire seed; in var. *demota* the seeds are usually broadly oblong with the winging only at the distal position and along one side.

Descurainia torulosa Rollins, sp. nov.

Herba multicaulis, humifusis; caulibus tenuibus, procumbentibus, dense pubescentibus, 6–10(–13) cm longis; foliis radicalibus petiolatis, lobatis, 2–3 cm longis; foliis caulinis paucis reductis; floribus minutis; pedicellis fructiferis appressis, erectis, 1.5–2.5 mm longis; siliquis linearibus, teretibus, dense pubescentibus, erectis, torulosis, 8–12(–15) mm longis, ca. 1 mm latis; stylis tenuibus, ca. 0.2 mm longis; seminibus anguste oblongis, exalatis, ca. 1.3 mm longis, ca. 0.5 mm latis; cotyledonibus incumbentibus.

TYPE. Wyoming, Fremont Co., Wind River Range, near Brooks Lake, rocky slopes at the base of cliffs 2 mi NW of the lake, 10,000 ft alt., 8 July 1966, *R. W. Scott 761* (holotype, GH).

Biennial or possibly perennial with well-developed taproot and unbranched crown; pubescent throughout with dendritic, few- to many-branched trichomes; stems several to numerous, procumbent, arising from dense cluster of crown leaves, simple or branched, 6–10(–13) cm long. Crown leaves with petiole short; blade pinnately lobed, 2–3 cm long, primary lobes simple or with 1 or 2 subsidiary lobes. Cauline leaves few, similar to crown leaves. Flowers minute; sepals oblong, nonsaccate, slightly more than 1 mm long, with hyaline margin all around, pubescent; petals spatulate, ca. 1.5 mm long, whitish. Fruiting pedicels erect, appressed to rachis, 1.5–2.5 mm long; siliques erect and appressed to rachis, curved outward to nearly straight, terete, linear, torulose, tapered below and toward apex, 8–12(–15) mm long, slightly more than 1 mm in diameter, the style slender, ca. 0.2 mm long, smaller in diameter than stigmatic area, usually pubescent. Seeds in single row, narrowly oblong, plump, ca. 1.3 mm long, wingless, ca. 0.5 mm in diameter, dark brown; radicle slightly longer than cotyledons; cotyledons incumbent.

As Detling (1939) pointed out, there are two principal growth types found in North American *Descurainia* Webb & Berthelot: one in which the single stem branches only well above the middle, resulting in a wandlike appearance; the other with branching beginning near the base of the single stem and with the numerous erect branches nearly equal to the leader, giving a bushlike aspect to the plants. A third growth type, found in a number of South American species, is characterized by several to many more or less equal stems arising from the crown of a taproot. The stems are erect in some of these species and procumbent in others. Several of the South American species are definitely perennial, whereas all heretofore-known North American species are annuals or biennials. In habit, *Descurainia torulosa,* unlike any known North American species, shares the characteristics of those South American species with procumbent stems. This species is probably perennial rather than biennial: the taproot with its crown is well developed, and the available specimens look as though they could be perennial, but one cannot be sure from the specimens alone. In addition to its distinctive branching habit, *D. torulosa* grows so low that it does not resemble any other North American species. Also, the closely appressed but flaring torulose siliques and the extremely short pedicels characteristic of *D. torulosa* are not matched in material of other species.

Draba hitchcockii Rollins, sp. nov.

Herba perennis, caespitosa; caudicibus ramosis; caulibus scapiformibus, erectis, hirsutis, (2–)3–7(–9) cm altis; foliis rosulatis, spathulatis vel oblongis, ciliatis, (3–)4–7(–10) mm longis, (1–)1.5–2 mm latis; sepalis late oblongis, hirsutis, ca. 3 mm longis; petalis late obovatis, albis, 5–6 mm longis, ca. 4 mm latis; pedicellis rectis, hirsutis, adscendentibus, (4–)6–10(–12) mm longis; siliquis erectis, ellipticis vel late oblongis, pubescentibus (4–)5–7(–8) mm longis, (3–)3.5–4.5(–5) mm latis; stylis 1.5–2 mm longis; seminibus oblongis, ca. 1.8 mm longis; cotyledonibus accumbentibus.

TYPE. Idaho, Butte Co., S Lost River Range, T7N, R26E, S17, N side of Elbow Canyon, 23 May 1982, *A. F. Cholewa 851* (holotype, GH; isotypes, ID, NY, and others to be distributed).

Perennial; caespitose; caudex loosely branched but forming clusters up to 1 dm in diameter; branches covered with remnants of old leaves and leaf-bases, terminating in dense, recent leaf-clusters. Leaves nonpetiolate, spatulate to oblong, (3–)4–7(–10) by (1–)1.5–2 mm, obtuse, 1-nerved, ciliate on margins and upper surface with large, simple (rarely forked) trichomes, marginal trichomes often as long as leaf width, lower surface with coarse, forked to 4-branched trichomes. Scapes slender, erect or outer slightly decumbent at base, (2–)3–7(–9) cm tall, leafless, hirsute with mixture of long, simple or forked trichomes and shorter, many-branched ones; sepals broadly oblong, ca. 3 mm long, hirsute with simple or forked trichomes; petals broadly obovate, 5–6 by ca. 4 mm, pure white, blade sharply constricted to narrow claw; stamens subequal, filaments slightly dilated at base. Infructescences racemose, subcorymbose to more elongated; pedicels straight, ascending to divaricately ascending, (4–)6–10(–12) mm long, hirsute; siliques erect, elliptic to broadly oblong or nearly ovate, (4–)5–7(–8) mm by (3–)3.5–4.5(–5) mm, densely pubescent with simple or forked trichomes, the styles 1.5–2 mm long, the ovules 4 to 6 in each loculus, the funiculi less than 0.5 mm long. Seeds oblong, plump, wingless, ca. 1.8 mm long; cotyledons accumbent.

REPRESENTATIVE SPECIMENS. **Idaho.** BUTTE CO. Lost River Range: Anderson Canyon ca. 11 mi N of Arco, *S. & P. Brunsfeld 859* (GH[1]); Arco Hills area, *Reese 138, 147, 148* (GH); Elbow Canyon, *Henderson 4959* (GH); Elbow Canyon ca. 12 mi E of Mackay, *S. & P. Brunsfeld 810* (GH, NY); Cedarville Canyon, north fork, *S. & P. Brunsfeld 1102* (GH); E slope just above bottom of Jaggles Canyon, ca. 1¼ mi above entrance, *Henderson 4993* (GH); Maddock Canyon, *S. & P. Brunsfeld 821* (GH, NY), *Henderson 4979* (GH); N of Sands Canyon, *B. Anderson 29* (GH). CUSTER CO.: Lost River Range, Waddoup's Canyon, *Reese 172* (GH).

This species was named for C. L. Hitchcock, monographer of western North American *Draba* and long-time student of the flora of the Pacific Northwest.

Although *Draba hitchcockii* has white flowers, it is undoubtedly most closely related to the yellow-flowered *D. paysonii* Macbr. var. *paysonii*, which occurs in Montana and Wyoming. It also differs from that species in having longer styles, more uniformly large simple trichomes on the leaf margins and the upper leaf-surfaces, and usually longer, more slender scapes. *Draba hitchcockii* differs even more from *D. paysonii* var. *treleasii* (Schulz) C. L. Hitchc. The latter is more widespread than var. *paysonii* and occurs in the general area of Idaho where *D. hitchcockii* is found, but usually at higher elevations. Although flower color is of little or no taxonomic significance in many genera of the Cruciferae, it is an important taxonomic character in *Draba* L. When correlated with other features, it can be utilized to distinguish taxa at the specific and infraspecific levels.

The fruits of *Draba hitchcockii* and *D. paysonii* var. *paysonii* are similar in size and in the pubescence on the valve surfaces, with the trichomes either simple (especially on the silique margins) or a combination of simple and forked. In some plants of *D. hitchcockii*, only simple trichomes are found on

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[1] Most, if not all, of the collections cited are probably also represented at the University of Idaho Herbarium (ID), but this has not been verified.

the entire silique. The shape of the siliques is different in the two taxa: in *D. hitchcockii* they are usually elliptic (rarely narrowly elliptic or nearly broadly ovate); in var. *paysonii* they are always broadly ovate. I have not seen any material of var. *paysonii* with anything other than a short subcorymbose infructescence, whereas in *D. hitchcockii* the infructescence is almost always racemose and is often somewhat elongated. The short stout scape and strongly condensed habit in var. *paysonii* contrast with the slender elongated scapes and the loose habit in *D. hitchcockii.*

I am indebted to Dr. Douglass Henderson, of the University of Idaho, for the following information on the plant associates and habitat of *Draba hitchcockii.* All populations are on thin soil in rocky limestone areas that range from steep to gently sloping. Accompanying species include *Leucopoa kingii* (S. Watson) W. A. Weber, *Agropyron spicatum* (Pursh) Scribner & Sm., *Cercocarpus ledifolius* Nutt. var. *intercedens* C. Schneider, *Pseudotsuga menziesii* (Mirbel) Franco, *Artemisia tridentata* Nutt., *A. arbuscula* Nutt. var. *nova* (A. Nelson) Cronq., *Phlox hoodii* Richardson, *Draba oreibata* Macbr. & Payson, and *D. densifolia* Nutt. *Cercocarpus* and *Artemisia* are the most important woody genera. Although *Draba hitchcockii* occurs at elevations from 5500 to ca. 7200 ft, most populations grow between 6000 and 6900 ft.

Draba pennellii Rollins, sp. nov.

Herba perennis, caudicibus ramosis; foliis radicalibus, pubescentibus, oblongis, acutis, 5–8 mm longis, ca. 2 mm latis; foliis caulinis 2–5, sessilibus, pubescentibus; caulibus tenuis, erectis, pubescentibus, 4–7 cm altis; pedicellis rectis, divaricatis, pubescentibus, 5–8 mm longis; sepalis oblongis, pilosis; petalis albis, obovatis, 4.5–6 mm longis; siliquis anguste ovatis, pubescentibus, ca. 5 mm longis; stylis ca. 2 mm longis; seminibus ignotis.

TYPE. Nevada, White Pine Co., Shell Creek Range, at head of South Fork of Berry Creek, on rock ledges, 10,000 to 10,500 ft alt., 13 July 1938, *F. W. Pennell & R. L. Shaeffer, Jr. 22977* (holotype, GH).

Perennial with loosely branching caudex; caudex branches elongated, partially covered with old leaves and leaf-bases, both sterile and fertile branches present in each clump; leaf-clusters elongated. Leaves nonpetiolate, oblong, 5–8 by ca. 2 mm, acute, entire, 1-nerved, densely covered with stalked, 4- or 5-branched, coarse trichomes, upper surface sometimes nearly glabrous. Flowering stems slender, simple, erect, 4–7 cm tall, densely pubescent with spreading dendritic, forked, or occasionally simple trichomes, simple trichomes increasing in frequency toward inflorescence; pedicels divaricately ascending, straight, densely pubescent with coarse, mostly dendritic and forked but occasionally simple trichomes; sepals oblong, ca. 3 by ca. 1.2 mm, greenish then turning purplish and with hyaline margin in age, sparsely covered on exterior with coarse, simple or forked trichomes; petals obovate, 4.5–6 by 3–4 mm, abruptly narrowed to short claw less than 1 mm long, truncate to shallowly retuse, white; stamens subequal, filaments dilated toward base. Siliques flattened, ovate to nearly oval, sometimes slightly asymmetric, ca. 5 by ca. 3 mm, moderately pubescent with minute forked (or simple) trichomes; styles ca. 2 mm long. Mature seeds not available.

SPECIMENS EXAMINED. **Nevada.** WHITE PINE CO.: 20 mi N of Ely, North Shell Peak, 11,800 ft alt., *Lavin 4209* (GH); Shell Creek Range, Steptoe Creek road, 9.3 mi E of U. S. Highway 93, *H. K. Sharsmith 4823* (GH).

Because cauline leaves are present on the flowering stems of both species, it is tempting to suggest that *Draba arida* C. L. Hitchc. is the closest known relative of *D. pennellii.* However, *D. arida* has rosulate basal leaves, closely branched or unbranched caudices, and only one or a few flowering stems per plant. Plants of *D. pennellii* are entirely different, consisting of numerous elongated caudex branches and basal leaves that are in elongated tufts. The number of flowering stems per plant ranges from several to many, but it is difficult to assess this feature accurately from specimens alone because the plants are tufted in cracks of rocks, making collection of a complete plant difficult. Collectors usually break off individual caudex branches. The habit of growth is much like that of *D. sphaeroides* Payson, and I am inclined to associate *D. pennellii* with that species. In both species there is stem elongation, forming well-defined internodes both between individual leaves and between tufts of leaves. Often new branches arise in the axils of individual leaves, and either these terminate in a cluster of sterile leaves, or a fertile branch arises at the terminal end of the cluster, forming an inflorescence toward its apex. The flowers of both *D. sphaeroides* and *D. arida* are yellow, while those of *D. pennellii* are pure white. The trichomes of all three species are fairly similar and cannot be relied upon as identifying characters. In *D. pennellii* the petal is distinctively shaped, with the broad, full blade narrowing abruptly to a very short claw. Neither in *D. sphaeroides* nor in *D. arida* is there a sharp differentiation into blade and claw: the blade narrows very gradually from the widest point at the apex to the point of insertion.

As compared to *Draba sphaeroides, D. pennellii* has fertile stems with 2 to 5 leaves (vs. a leafless scape); white, obovate petals that are sharply differentiated into blade and claw (vs. yellow, spatulate, and gradually tapered from blade to claw); and dense pubescence extending up the fertile stems to include the pedicels of the infructescence (vs. the upper portion of the fertile stems and pedicels glabrous). In both species the siliques are either pubescent with minute forked or simple trichomes, or glabrous.

Lesquerella goodrichii Rollins, sp. nov. FIGURE 3.

Herba perennis; caudicibus ramosis densis; caulibus decumbentibus vel erectis, tenuibus, 8–14 cm longis; foliis radicalibus erectis, dense pubescentibus, argenteis, petiolatis, (1.5–)2–4(–6) cm longis, (3–)4–7(–10) mm latis; foliis caulinis integris, anguste spathulatis, cuneatis; sepalis viridis vel argenteis, pubescentibus, oblongis, nonsaccatis, ca. 5 mm longis, ca. 1.8 mm latis; petalis spathulatis, aureis, 7–9 mm longis, 2.5–3 mm latis; pedicellis divaricatis, sigmoideis vel fere rectis, pubescentibus, 4–6 mm longis; siliquis erectis, compressis, ellipticis, 4–5 mm longis, ca. 3 mm latis; stylo 3–4 mm longo; loculis 2–4 ovulatis; seminibus immaturis exalatis; cotyledonibus accumbentibus.

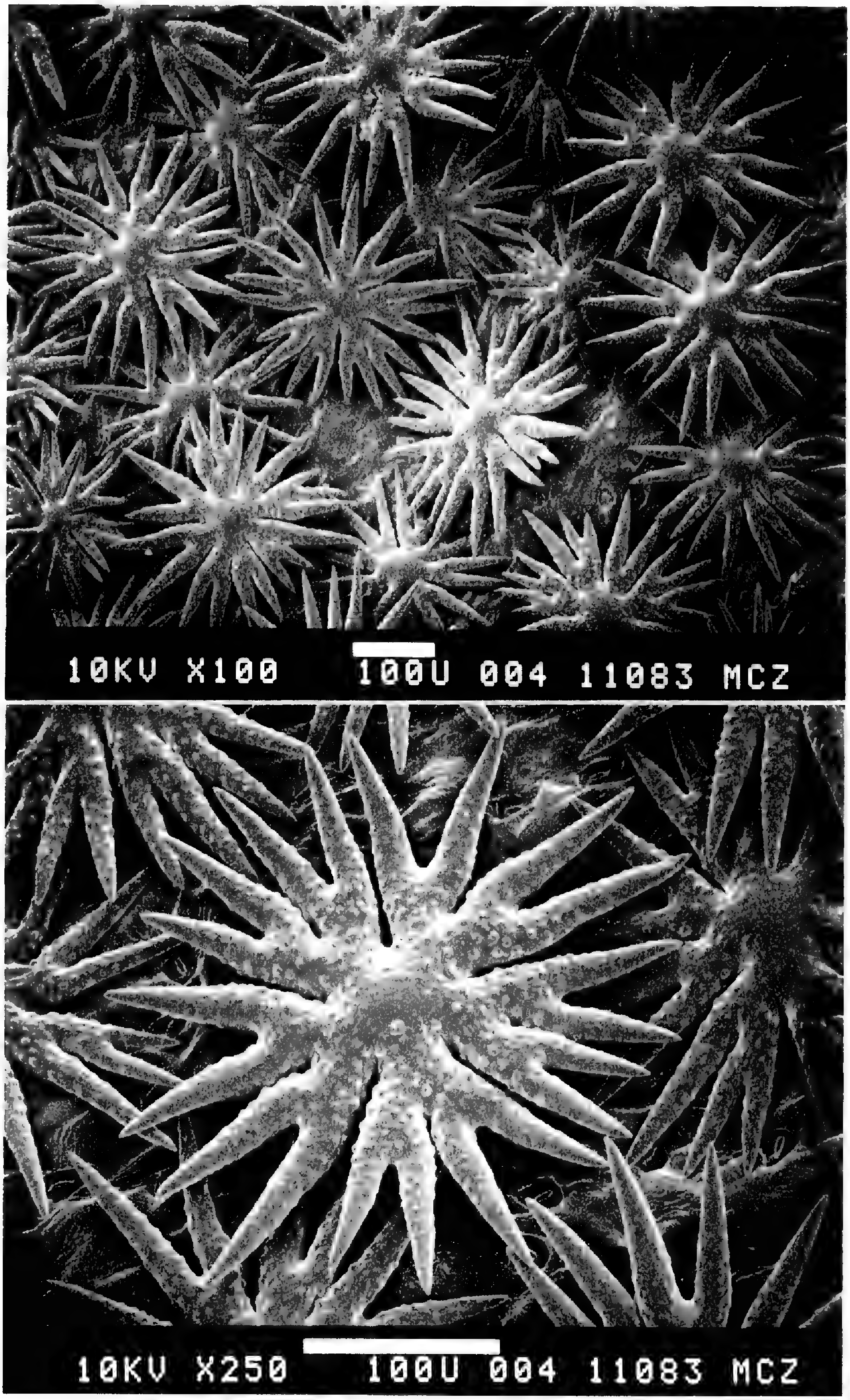

FIGURE 3. SEM photos of trichomes of **Lesquerella goodrichii** (*Goodrich 16951*): above, spacing of trichomes on leaf-surface; below, enlargement of single trichome.

TYPE. Utah, Millard Co., Desert Experimental Range, Tunnel Springs Mts., 21 mi SE of Garrison, T24S, R17W, S9, steep slopes and ridges, mostly N exposure, 8000 ft alt., 16 June 1982, *S. Goodrich 16951* (holotype, GH; isotypes, BRY, NY, UTC).

Perennial, densely covered throughout (except on petals and styles) with appressed radiate trichomes; caudex closely branched, branches usually covered with old leaf-bases; stems several to many, slender, simple, mostly decumbent, 8–14 cm long. Basal leaves numerous, erect, (1.5–)2–4(–6) cm by (3–)4–7(–10) mm; petiole to 3 cm long, slender; blade oblanceolate and entire to deltoid with broad tooth on each side. Sepals oblong, nonsaccate, ca. 5 by ca. 1.8 mm, greenish to silvery; petals erect, spatulate, not differentiated into blade and claw, 7–9 by 2.5–3 mm, yellow. Fruiting pedicels divaricately ascending to widely spreading, sigmoid to nearly straight, 4–6 mm long; siliques erect, elliptic, strongly compressed parallel to septum, 4–5 by ca. 3 mm, the valves densely pubescent on exterior, glabrous on interior, the septum entire, the replum elliptic, acute at apex, the style 3–4 mm long, slender, with expanded stigma, glabrous or with 1 or 2 trichomes near base; ovules 2 to 4 in each loculus, attached above middle of replum. Immature seeds wingless, often crowded and misshapen; cotyledons accumbent.

SPECIMENS EXAMINED. **Utah.** MILLARD CO.: Desert Experimental Range, 20 mi SE of Garrison, T24S, R17W, S3, 7200 ft alt., *Goodrich 16539* (BRY, GH); Canyon Mts., Lyman Canyon, 7.75 mi E of Oak City, T17S, R3W, S16, 8000 ft alt., *Goodrich 16883* (BRY, GH, NY, UTC), *Goodrich 17949* (BRY).

The strongly flattened siliques of *Lesquerella goodrichii* indicate a close relationship to *L. occidentalis* S. Watson, and these two species are indeed similar in many respects. However, the trichomes are decidedly different: in *L. occidentalis* they are stellate with radiating branches, have slender, elongated, very gradually tapering tips, and are free to their bases or nearly so; in *L. goodrichii* they have comparatively massive branches and branch bases, the tips contract abruptly to a point, and there is considerable fusion toward the center of each trichome. (See FIGURE 3. For comparison, see *plates 2* and *16* in Rollins & Banerjee, 1975—SEM pictures of trichomes of *L. occidentalis* subspp. *occidentalis* and *cinerascens.*)

Plants of *Lesquerella occidentalis* are more robust and have thicker stems and longer infructescences than those of *L. goodrichii*, which are usually delicate, with slender stems and narrow, short infructescences. The pedicels of *L. goodrichii* tend to be weakly sigmoid and erect or at least ascending, while those of *L. occidentalis* are strongly sigmoid and are more at right angles to the rachis or even descending. The long, slender petioles and relatively short blades of the numerous basal leaves of *L. goodrichii* are distinctive features of this species.

It is with some hesitation that I have cited the two collections from the Canyon Mountains under *Lesquerella goodrichii*. Although these plants have the same trichome type as those from the Desert Experimental Range, the leaf-blades are much broader and of a different shape, and they usually have two broad teeth instead of being entire. The two localities are at some distance from each other even though they are in the same county. Additional material with mature fruits is required from the Canyon Mountain area to see whether a minor taxon should be recognized under *L. goodrichii.*

Lesquerella parviflora Rollins, sp. nov.

Herba perennis multicaulis; caulibus procumbentibus vel adscendentibus, 1–3 dm longis; foliis radicalibus late obovatis, petiolatis, argenteis, sparse dentatis vel integris, 1–2 cm longis, 6–10 mm latis; foliis caulinis cuneatis, oblanceolatis vel oblongis, integris; sepalis oblongis, nonsaccatis, dense pubescentibus, 3–3.5 mm longis, ca. 1.5 mm latis; petalis spathulatis, flavis, 5–6 mm longis, 2–2.5 mm latis; pedicellis fructiferis recurvatis, 6–8(–12) mm longis; siliquis ellipticis vel prope globosis, dense pubescentibus, 3–4 mm longis, 2.5–3 mm latis; stylo glabro, ca. 3 mm longo; loculis 2-ovulatis; seminibus late oblongis vel prope orbicularibus, 2.5–3 mm longis, ca. 2.5 mm latis; cotyledonibus accumbentibus.

TYPE. Colorado, Rio Blanco Co., USGS Black Cabin Gulch Quadrangle, T3S, R100W, S13, ¾ mi S of spring in Tommy's Draw, 2595 m alt., 21 July 1982, *W. Baker & S. Sigstedt 82-308* (holotype, GH; isotype, CS).

Perennial, silvery from dense covering of stellate trichomes; stems several to numerous, prostrate to ascending, simple or rarely branched above, 1–3 dm long. Basal leaves tufted, petiolate, 1–2 cm by 6–10 mm; blade broadly obovate, rounded to obtuse, entire or with 1 or 2 broad teeth, silvery. Cauline leaves oblanceolate to nearly oblong, cuneate at base, entire. Sepals oblong, nonsaccate, 3–3.5 by ca. 1.5 mm, densely pubescent; petals erect, spatulate, scarcely differentiated into blade and claw, 5–6 by 2–2.5 mm, yellow; anthers nearly oval, ca. 1 mm long. Infructescences rather dense, ⅓–½ of stem length; fruiting pedicels recurved, 6–8(–12) mm long, densely pubescent; siliques mostly pendent, elliptic to nearly globose, usually slightly compressed parallel to septum, 3–4 by 2.5–3 mm or ca. 3 mm in diameter, densely pubescent on exterior, the valves glabrous or with few scattered trichomes on interior, the styles ca. 3 mm long, noncapitate, glabrous, the ovules 2 per locule, attached toward apex of replum, the septum entire, the replum nearly oval to obovoid in outline. Seeds oval to slightly longer than broad, somewhat compressed, wingless, 2.5–3 by ca. 2.5 mm; cotyledons broadly oblong to nearly orbicular, accumbent.

SPECIMENS EXAMINED. **Colorado.** RIO BLANCO CO.: USGS Segar Mountain Quadrangle, T1S, R96W, S1, 1 mi SSW of junction of Hay Gulch and White R., 1905 m alt., *Baker & Naumann 82-231* (CS, GH); USGS Philadelphia Creek Quadrangle, T1S, R100W, S21, 2.45 mi SSE of junction of West Fork Spring Creek and McDowell Gulch, 2316 m alt., *Kelley & Naumann 82-155* (CS, GH); Cathedral Bluff Rim Road, Piceance Basin, lat. 39°46′36″ N, long. 108°33′38″ W, *Peterson et al. 1141* (CS), *Painter et al. 132* (CS); USGS Jessup Gulch Quadrangle, T2S, R96W, S21, 2.2 mi NNE of junction of Collins Gulch and Piceance Creek, *Walker & Naumann 82-213* (CS); T3S, R100W, S24, NE ¼, 1.8 km NE of confluence of Lake Creek and Cathedral Creek, Parachute Creek Member of Green River Formation, *Wilken 13866* (COLO, CS, GH, RM).

The recurved pedicels of *Lesquerella parviflora* are similar to those of *L.*

arenosa (Richardson) Rydb. and *L. ludoviciana* (Nutt.) S. Watson, and the siliques of these three species are somewhat alike. The most fundamental differences between *L. parviflora* and the other two species are in ovule number and in the position of the funiculi on the replum of the silique. In *L. parviflora* there are only two ovules per locule and the two funiculi are restricted to an area near the apex of the replum; in both *L. arenosa* and *L. ludoviciana* the number of ovules is variable, ranging from four to eight in each locule, and the funiculi are arranged not only toward the apex of the replum but down the sides as well. Although the trichomes of all three species are stellate, with four to six primary rays (each of which is forked or bifurcate to provide anywhere from ten to twenty free tips), those of *L. parviflora* are smaller, with shorter, more massive, more tapered ultimate branches and a greater amount of fusion toward the center of the trichome than is found in the other two species. Characteristically, the trichomes are spreading on the siliques of *L. arenosa* and *L. ludoviciana,* while they are closely appressed in *L. parviflora.* There is a sharp difference in the shape of the basal leaves: in *L. arenosa* and *L. ludoviciana* the inner basal leaves are linear or nearly so with a scarcely differentiated petiole, but in *L. parviflora* all of the basal leaves are distinctly differentiated into a comparatively broad blade and a short petiole.

A significant feature of *Lesquerella parviflora* is the presence in the inflorescences of short shoots subtended by leafy bracts. This is particularly evident in *Wilken 13866,* where many of the specimens are in flower. The only other species of *Lesquerella* known to have short shoots in the inflorescences are *L. argyrea* (A. Gray) S. Watson subsp. *diffusa* (Rollins) Rollins & E. Shaw and *L. peninsularis* Wiggins, both of which occur exclusively in Mexico.

Among the specimens of the seven collections of *Lesquerella parviflora* cited, there is considerable diversity, which is probably attributable in part to the habitat. *Baker & Sigstedt 82-308* was collected on shale ledges, implying an exposed habitat. Quite compact in the caudex area, these specimens have prostrate stems, narrow, dense infructescences, and short pedicels. The siliques are uniformly elliptic in outline and slightly compressed parallel to the septum. The specimens of *Baker & Naumann 82-231,* collected "on shale with *Ribes aureum* and *Pinus,*" show both decumbent and upright stems, looser infructescences, slightly longer pedicels, and elliptic to subglobose siliques. *Kelley & Naumann 82-155,* "common on slopes of canyon with *Acer, Prunus, Betula,* and *Agropyron,*" is made up of sprangly specimens with ascending, sparsely branched stems, loose infructescences, long pedicels, and elliptic siliques that are noticeably compressed parallel to the septum. From my experience and observations in the field involving other species of *Lesquerella,* it appears that the differences in habit shown by these collections probably reflect responses to habitat: in the first instance, a dry, open, possibly windswept area; in the second, a somewhat more protected locale; and in the third, probably a shady situation with deep soil and other conditions favoring more rapid growth than normally takes place in the more open habitats. The variation in silique shape noted in *Baker & Naumann 82-231* is probably genetic and reflects the type of diversity found between (not within) populations in other species of *Lesquerella.* This diversity cannot be explained from the material available.

Polyctenium williamsiae Rollins, sp. nov.

Herba perennis, caespitosa; caudicibus ramosis; foliis pectinatis, sparsim pubescentibus; caulibus erectis vel decumbentibus, simplicibus, 4–10 cm longis; inflorescentiis corymbosis; petalis obovatis vel spathulatis, truncatis, 3–3.5 mm longis, 1.8–2 mm latis, albis vel purpureis; infructescentiis elongatis; pedicellis adscendentibus vel divaricatis, rectis, pubescentibus, 3–5 mm longis; siliquis late oblongis, glabris, 3–4 mm longis, 2–2.5 mm latis; stylo ca. 0.5 mm longo; seminibus immaturis, oblongis, immarginatis.

TYPE. Nevada, Washoe Co., Virginia Range, T17N, R20E, S16, foothills E of Little Washoe Lake, edge of a vernal pond, 5680 ft alt., *A. Tiehm 7135 & M. Williams* (holotype, GH; isotypes to be distributed).

Perennial with taproot and with occasional underground root branches bearing retoños along their length; caudex loosely branched. Basal leaves densely tufted, stiff, pectinate, pubescent with mostly dendritically branched trichomes, these interspersed with larger, simple or forked trichomes; linear leaf segments often tipped with large, simple or forked trichomes. Cauline leaves similar to basal, sessile, nonauriculate. Inflorescences densely corymbose; sepals broadly oblong, ca. 2 mm long, hyaline margined, greenish to purplish, sparsely pubescent; petals obovate to broadly spatulate, truncate at apex, gradually tapering to point of insertion, 3–3.5 by 1.8–2 mm, whitish to purplish; anthers nearly orbicular, less than 0.5 mm long. Infructescences elongated; pedicels ascending to divaricately ascending, straight, 3–5 mm long, sparsely pubescent; siliques crowded, divaricately ascending, broadly oblong to nearly oval in outline, rounded above and below, 3–4 by 2–2.5 mm, compressed (usually unevenly) in plane opposite to that of septum, mostly glabrous, the styles thick, ca. 0.5 mm long, the stigma slightly expanded beyond diameter of style, the ovules 15 to 20 per locule, the funiculi slender, ca. 0.5 mm long. Immature seeds broadly oblong, plump, wingless.

Greene (1912), in setting up *Polyctenium* E. Greene as a genus distinct from *Smelowskia*, believed that it consisted of three species, *P. bisulcatum* E. Greene, *P. fremontii* (S. Watson) E. Greene, and *P. glabellum* E. Greene. However, it was later shown (Rollins, 1938) that all of the material then available, including the types of Greene's species, was referable to a single species consisting of two varieties. The first incontrovertible evidence that *Polyctenium* is not monotypic comes from the newly described *P. williamsiae*. Comparison of this species with the only other known species in the genus, *P. fremontii*, yields several differences. The siliques of *P. williamsiae* are broadly oblong to nearly oval—much shorter and wider and thus of a very different shape than the linear, much longer, narrower siliques of *P. fremontii*. The flowers of *P. williamsiae* are considerably smaller than those of *P. fremontii*. The styles of *P. williamsiae* are about half the length of those of *P. fremontii*. The dried leaves, stems, and siliques are greenish in *P. williamsiae* and gray in *P. fremontii*. The valves of the siliques in *P. fremontii* are smooth and rigid, while those of *P. williamsiae* are uneven, showing depressed areas that indicate a lack of rigidity in the valve wall.

The generic status of *Polyctenium* has been considerably strengthened by the discovery of a second species. Although Jepson (1936) and Abrams (1944) did not accept *Polyctenium,* the genus has been recognized in the more recent floras (e.g., Munz, 1959; Hitchcock & Cronquist, 1973) that cover the area where it occurs.

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GRAY HERBARIUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

THE MODERN NAMES FOR CATESBY'S PLANTS

RICHARD A. HOWARD AND GEORGE W. STAPLES

MARK CATESBY (1682–1749) collected plants in the southeastern United States from Maryland to Florida between 1712 and 1719 and again between 1722 and 1725 (Reveal, 1983). During part of 1725, before his return to England in 1726, he collected in the Bahama islands of New Providence, Abaco, Andros, and Eleuthera (Britton & Millspaugh, 1920). Dried specimens, as well as seeds and possibly living plants, were sent to correspondents and sponsors in England and Europe (Allen, 1937). Plants and animals were sketched in the field, and drawings were occasionally done from plants grown from seeds or under cultivation in Europe. Catesby (1731, p. xi) said, "As I was not bred a Painter I hope some faults in Perspective, and other Niceties may be more readily excused. . . ." Unfortunately, two drawings are so inaccurate that they still cannot be identified.

The Natural History of Carolina, Florida and the Bahama Islands, termed "a pioneer contribution to the natural history of the West Indies as well as to that of the southern United States" (Stearn, 1958, p. 328), was published in parts between 1730 and 1743, with an appendix appearing in 1747. The work was soon cited by J. F. Gronovius in his *Flora Virginica.* Linnaeus cited many but not all of Catesby's plates in *Species Plantarum* (ed. 1, 1753; ed. 2, 1762, 1763), *Systema Naturae* (ed. 10, 1759), *Centuria II. Plantarum* (1756; contains a single reference to *Vinca lutea*), *Mantissa Plantarum* (1767), and *Mantissa Plantarum Altera* (1771).

Catesby's plates appear to be the types of twenty-five recognized taxa, of which twenty-one were described by Linnaeus and four by subsequent authors. They are also the types of an additional twelve synonymous names. Typotype[1] specimens from the Sloane herbarium have been indicated for some species, primarily by Dandy (1958). Linnaeus may have seen some of Catesby's collections when he visited Gronovius (1735) or Sherard (1736). It is generally stated that the plate is the type, and supporting specimens "in the Sloane set can be associated with certain of the plates" (Stafleu, 1967, p. 78). Not all of Catesby's plates have been satisfactorily identified, in spite of existing listings. In a search of the Sloane herbarium (BM) and the Sherard and Du Bois herbaria (OXF), no specimens were found to aid in the identification of *plates 30, 45,* or *52* in volume two. Catesby's specimens are also known to occur in the general herbarium at the British Museum (Natural History). These are primarily from

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[1] Typotype: a specimen that served as the basis for a published illustration or description subsequently designated as the type of a validly published name. Typotype specimens have no nomenclatural standing but may be considered as supporting evidence in the interpretation of ambiguous or incomplete type descriptions or illustrations.

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the Gronovius and the Samuel Dale herbaria. Sir Joseph Banks had acquired the Gronovius herbarium, and the Dale herbarium had been presented to the Society of Apothecaries at the Chelsea Physic Garden. Both herbaria were acquired by the British Museum (Natural History). Catesby's own holographic notes, although commonly attributed to the Oxford collections, also occur on various specimens in London (BM).

A second edition of Catesby's *Natural History* was edited by George Edwards and published in 1754. A third edition, published in 1771, contained as an appendix credited to Edwards "A Catalogue of the Animals and Plants Represented in Catesby's Natural History of Carolina: with the Linnaean names." Also in 1771 Johann Reinhold Forster published a translation of J.-B. Bossu's *Travels Through that Part of North America Formerly Called Louisiana*, to which he added (Volume 2, pp. 17–67) "A Systematic Catalogue of all the Known Plants of English North-America, or, a Flora Americae Septentrionalis." Forster cited many but not all of Catesby's plates, with references to Linnaeus's works. It is possible that both Edwards and Forster obtained much of the information from the second edition of Gronovius's *Flora Virginica* (1762), where more of Catesby's plates are cited than in edition one and references are given to Linnaeus's *Species Plantarum*. Occasional references associating Catesby's plates with Linnaean names are also found in Adanson's *Familles des Plantes* (1763).

Modern names for Catesby's plants and plates have been suggested by various twentieth-century authors. The first comprehensive treatment was that by Britton and Millspaugh in *The Bahama Flora* (1920), where all but one of Catesby's plants from the Bahama Islands were identified under the then-accepted names. Regrettably, Catesby's polynomials were not listed in the index, and some of the suggestions of Britton and Millspaugh have therefore been overlooked by subsequent authors. In *The Sloane Herbarium* Dandy (1958) identified a few of Catesby's polynomials and plates and associated them with typotypes in that herbarium. Stevenson (1961) in a treatment of Catesby in volume two of the *Catalogue of Botanical Books in the Collection of Rachel McMasters Miller Hunt*, suggested a few identifications. In 1974 the Beehive Press, Savannah, Georgia, issued a partial facsimile of Catesby's work, with reproduction of a number of the colored plates together with the related text. An accompanying volume contains an historical introduction by George Frick, notes by Joseph Ewan, and black and white reproductions of all the plates. Ewan suggested determinations of all of the plants and birds illustrated by Catesby, but we do not agree with all of his names. Since the facsimile reproduction and the text have not been widely distributed and no reprints of the folio-sized text are available, we believe that the following lists and comments should be useful.

Catesby's collections (BM, OXF) (Clokie, 1964) are more extensive than those illustrated in his *Natural History*. These have not been cited, to our knowledge, and have no bearing on modern nomenclature, but they are of interest since some represent introduced taxa or give clues to his collecting localities. The search for typotype specimens of the species illustrated involved all of the specimens in volumes 212 and 232 of the Sloane herbarium (BM), and are so cited. Commonly mounted with other collections, the specimens are small or fragmentary and may occur on several pages. The Sherard and Du Bois herbaria (OXF) are retained as historic herbaria, often without separation to modern families or genera. A large number of Catesby's specimens with holographic notes were found in the unidentified material at Oxford; these have been annotated, with a decision pending where they will be filed.

This work began with the need for the modern nomenclature of Catesby's illustrations. These were cited in an unpublished manuscript of Alexander Anderson, the second director of the St. Vincent Botanical Garden (1785–1811), who introduced Bahama plants to that garden and supplied binomials himself. The work on Anderson, including visits to London and Oxford, was supported by a much-appreciated grant to the senior author by the Stanley Smith Horticultural Trust. We are also grateful to the curatorial staff at the British Museum (Natural History) and the Fielding-Druce Herbarium at Oxford. We particularly value the comments of Charles Jarvis (BM, LINN), who is endeavoring to typify the Linnaean taxa in *Species Plantarum*. Our cooperative colleague, Dr. Leslie Garay, supplied the identifications of the Orchidaceae.

In the following notes, the plants that Catesby described and illustrated have been arranged alphabetically by families and genera. All names that we have determined to be based on Catesby's illustrations are marked with an asterisk. The plants are cited as plates by volume and number—for example (**1:** *t. 11*). Catesby's descriptive phrases in Latin and his common names are given, with spelling, punctuation, and capitalization as in the first edition of *Natural History*. Comments are made on the typification. Associated specimens are cited for the Sloane herbarium (H.S.), the general herbarium of the British Museum of Natural History (BM), the Dale herbarium (BM-Dale), the Sherard herbarium (OXF-S), and the Du Bois herbarium (OXF-DB). A list is supplied, numerically arranged, with our suggested identifications of plates in volumes 1 and 2, including the Appendix.

GYMNOSPERMAE

TAXODIACEAE

Taxodium distichum (L.) Rich. (**1:** *t. 11*)

Cupressus Americana. Cypress of America.

Cupressus disticha L. Sp. Pl. 1003. 1753. Catesby, Hortus Upsal., Gronovius, and others are cited. (H.S. 212, f. 4 (left); 232, f. 69, f. 85.)

ANGIOSPERMAE - MONOCOTYLEDONEAE

AMARYLLIDACEAE

Hymenocallis caroliniana (L.) Herb.* (2(App.): *t. 5*)

Lilio-Narcissus Polianthus, flore albo.

Pancratium carolinianum L. Sp. Pl. 291. 1753. Linnaeus cited only Catesby. Dandy (1958, p. 112) noted that the plate is the type. Sealey (Kew Bull. **1954:** 234–236) commented on the illustration and recognized the species under *Hymenocallis,* but noted that it had not been re-collected in the area where Catesby is known to have traveled. It is represented by only a single collection. No current floras of the southeastern United States recognize the species, but it is listed in Correll and Johnston (Manual of the Vascular Plants of Texas, 1970) for Texas.

Zephyranthes atamasco (L.) Herb. (**2**(App.): *t. 12*)

Lilio narcissus Virginiensis. Attamusco Lily.

Amaryllis atamasca L. Sp. Pl. 292. 1753. Catesby, Hortus Cliffort., Gronovius, and others were cited. (BM-Dale.)

ARACEAE

Orontium aquaticum L. (**1**: *t. 82*)

Arum aquaticum minus; S. Arisarum fluitans pene nudo Virginianum.

Orontium aquaticum L. Sp. Pl. 324. 1753. Catesby was not cited.

Peltandra virginica (L.) Schott & Engler (**1**: *t. 83*)

Arum Sagitariae folio angusto, acumine & auriculis acutissimis.

Ewan (1974, p. 94) identified this illustration as *P. sagittaefolia* (Michx.) Morong, which has a white spathe and red berries.

Symplocarpus foetidus (L.) Nutt. (**2**: *t. 71*)

Arum Americanum, Betae folio. Scunk Weed.

Dracontium foetidum L. Sp. Pl. 967. 1753. Catesby was not cited.

Unidentified *Alocasia* or *Xanthosoma* (**2**: *t. 45*)

Arum maximum Aegyptiacum, quod vulgo Colocasia.

The plate shows an inflorescence and a folded leaf, neither of which represents *Colocasia esculenta* (L.) Schott, the identification suggested by Ewan (1974). Catesby stated:

> The roots of this Plant are tuberous, with many small Fibres growing from them; some of them weigh six or eight Pound, of an irregular Form, the Outside of a rusty brown colour, the Inside white. The Leaves grow out of the Earth, with only their Foot-stalks, to the Height of four or five Feet; they are shaped somewhat like a Heart, of a pale Green, very ample, some of them being two Feet wide, and more in Length. The Flower in Form resembles that of the common *Arum,* tho' in Colour different, the Hood is green without, and of a light yellow within; the Pistil is long and slender, of a light purple Colour.
>
> Sir *Hans Sloane,* has so amply treated of this useful Plant, that I shall ask Leave only to add a few Remarks more. It is a Tropick Plant, not caring to encrease much in *Carolina,* and will grow no where North of that Colony; yet the Negro's there (who are very fond of them) by annually taking up the Roots to prevent rotting, get a small Encrease: They are of so acrimonious a Quality, that there is a Necessity of boiling them eight or ten Hours before they are eatable. A little before I left *Carolina,* there was introduced a new Kind, wholly without that bad Quality, and requiring no more than common Time to boil them, and may be eat raw, without offending the Throat or Palate; this was a welcome Improvement among the Negro's, and was esteemed a Blessing; they being delighted with all their *African* Food, particularly this, which a great Part of *Africa* subsists much on.

This later introduction may be *Colocasia esculenta* (L.) Schott.

BROMELIACEAE

Catopsis berteroniana (Schultes) Mez (**2**: *t. 77*)

Viscum Caryophylloides, Aloës foliis viridibus acuminatis, floribus racemosis luteis.

Tillandsia balbisiana (Schultes) Roemer & Schultes (**2**: *t. 89*)

Viscum Cariophylloides angustifolium, Floribus longis tubulosis caeruleis, ex spicis squamosis caeruleis erumpentibus. Wild Pine.

COMMELINACEAE

Commelina virginica L. (**2:** *t. 62*)

Pseudo-Phalangium ramosum.

Commelina virginica L. Sp. Pl. ed. 2. 61. 1762. Catesby was not mentioned. (H.S. 212, f. 6, f. 57.)

GRAMINEAE

Oryza sativa L. (**1:** *t. 14*)

Rice.

Oryza sativa L. Sp. Pl. 333. 1753. Catesby, Hortus Cliffort., and others were cited.

Uniola paniculata L. (**1:** *t. 32*)

Gramen Myloicophoron Oxyphyllon Carolinianum, &c. Sea-side Oat.

Uniola paniculata L. Sp. Pl. 71. 1753. Catesby, Hortus Cliffort., and Gronovius were cited.

HYDROCHARITACEAE

Thalassia testudinum König (**2:** *t. 38*)

Alga marina, graminea angustissimo folio.

Catesby was not cited by König. (H.S. 232, f. 13.)

HYPOXIDACEAE

Hypoxis sp. (**1:** *t. 33*)

Ornithogalum luteum parvum folijs gramineis glabris. Little yellow Star-Flower.

Ewan (1974, p. 92) cited this illustration as *Hypoxis hirsuta* (L.) Cav., which is based on *Ornithogalum hirsutum* L. (Sp. Pl. 306. 1753). Linnaeus did not cite Catesby. No supporting specimen could be found, and the plant may well be *Hypoxis juncea* J. E. Sm.

LILIACEAE

Lilium canadense L. (2(App.): *t. 11*)

Lilium sive Martagon Canadense, floribus magis flavis, non reflexis.

Lilium canadense L. Sp. Pl. 303. 1753. Catesby, Morison, and others were cited.

Lilium catesbaei Walter (**2:** *t. 58*)

Lilium Carolinianum, flore croceo punctato, petalis longioribus & angustioribus. Red Lilly.

Catesby was not mentioned in Walter's description (Fl. Carolin. 123. 1788).

Lilium philadelphicum L. (2(App.): *t. 8*)

Lilium angustifolium, flore rubro singulari.

Lilium philadelphicum L. Sp. Pl. ed. 2. 435. 1762. Catesby was not mentioned in the original description, and the type is presumably Miller, Fig. Pl. Gard. Dict. **2:** *t. 165, fig. 1.* 1760.

Lilium superbum L. (**2:** *t. 56*)

Lilium, sive Martagon Canadense, flore luteo punctato.

Lilium superbum L. Sp. Pl. ed. 2. 424. 1762. Miller, Trew, Ehret, and Catesby were cited. Ewan (1974, p. 97) called this illustration *Lilium michauxii* Poiret.

Trillium catesbaei Ell.* (**1:** *t. 45*)

Solanum triphylion flore hexapetalo carneo.

Catesby was not mentioned in the original description (Sketch Bot. S.-Carolina Georgia **1:** 429. 1817). Dandy (1958, p. 112) stated that the plant is *Trillium catesbaei* Ell., with a typotype specimen H.S. 212, f. 59 (flower, lower row, second from right). See also A. B. Rendle (Jour. Bot. London **39:** 322–325. 1901).

Trillium maculatum Raf.* (**1:** *t. 50*)

Solanum triphyllon flore hexapetalo tribus petalis purpurejs erectis coeteris viridibus reflexis.

Linnaeus cited Catesby, Gronovius, and Plukenet in the protologue of *Trillium sessile* L. (Sp. Pl. 340. 1753). Dandy (1958, p. 112) stated that Catesby's illustration is *Trillium maculatum* Raf., with a typotype H.S. 212, f. 59 (flower, lower right), and this selection has been confirmed by J. D. Freeman (Brittonia **27:** 27. 1975).

ORCHIDACEAE

Cleistes divaricata (L.) Ames (**1:** *t. 58, above*)

Helleborine Lilijfolio caulem ambiente, flore unico hexapetalo, tribus petalis longis angustis obscurè purpureis, caeteris brevioribus roseis. Lilly-leaf'd Helebore.

Arethusa divaricata L. Sp. Pl. ed. 2. 1346. 1763. Catesby and Gronovius were cited.

Cypripedium acaule Aiton (**2:** *t. 72*)

Helleborine. Lady's Slipper of *Pensilvania.*

Ewan (1974, p. 98) identified this illustration as *Cypripedium calceolus* L. The plate is also the type of *Cypripedium vittatum* Vell. var. *planum* Raf. (Herb. Raf. 44. 1833).

Cypripedium acaule Aiton (**2**(**App.**): *t. 3*)

Calceolus, flore maximo rubente, purpureis venis notato, foliis amplis hirsutis crematis, radice dentis canini.

This illustration is the type of *Cypripedium catesbianum* Raf. (Herb. Raf. 44. 1833). Rafinesque cited the third edition of Catesby (1771), with this plate as "*t. 103.*"

Cypripedium pubescens Willd. (**2:** *t. 73*)

Calceolus Marianus glaber, Petalis angustis. Yellow Lady's Slipper.

Ewan (1974, p. 98) referred this illustration to *Cypripedium calceolus* L. var. *pubescens* (Willd.) Correll. The plate is also the type of *Cypripedium vittatum* Vell. var. *tortile* Raf. (Herb. Raf. 44. 1833).

Epidendrum boothianum Lindley (**2:** *t. 74*)

Viscum Caryophilloides, floribus parvis luteis punctatis.

Ewan (1974) identified this illustration as *Epicladium boothianum* (Lindley) Small.

Epidendrum cochleatum L. (**2:** *t. 88, right*)

Viscum Caryophylloides, Lilii albi foliis, Floris labello brevi purpureo, ceteris Petalis ex luteo virescentibus.

Epidendrum cochleatum L. Sp. Pl. ed. 2. 1351. 1763. Sloane, Catesby, and Plumier were cited. The Plumier reference (Burman, Pl. Am. 180. *t. 185, fig. 2.* 1759) has been chosen as the lectotype.

Epidendrum nocturnum Jacq. (**2:** *t. 68*)

Viscum Caryophylloides, foliis longis in apice incisis, floris labello albo trifido, petalis luteis, longis angustissimis.

Epidendrum nocturnum L. Sp. Pl. ed. 2. 1349. 1763. Catesby and Jacquin (Select. Stirp. Am. Hist. *t. 139*) were cited. Jacquin's figure has been chosen as the lectotype.

Epidendrum plicatum Lindley (**2:** *t. 88, left*)

Viscum radice bulbosa; Floris labello carneo, ceteris sordide luteis.

Polystachya concreta (Jacq.) Garay & Sweet (**2:** *t. 55*)

Viscum Caryophylloides ramosum, floribus minimis albis.

Ewan (1974, p. 97) called this illustration *Polystachya minuta* (Aublet) Britton.

Vanilla mexicana Miller (**2**(App.): *t. 7*)

Volubilis siliquosa mexicana plantagini folio.

Epidendrum vanilla L. Sp. Pl. 952. 1753. Catesby and others were cited. Ewan (1974, p. 99) referred this illustration to *Vanilla planifolia* Andr.

SMILACACEAE

Smilax lanceolata L. (**2:** *t. 84, below*)

Smilax non Spinosa baccis rubris.

Smilax lanceolata L. Sp. Pl. 1031. 1753. Catesby was not cited. (OXF-DB, OXF-S.)

Smilax laurifolia L. (**1:** *t. 15*)

Smilax laevis, Lauri folio, baccis nigris. Bay-leaved Smilax.

Smilax laurifolia L. Sp. Pl. 1030. 1753. Catesby and Gronovius were cited. (OXF-S.)

Smilax pumila Walter (**1:** *t. 47*)

Smilax non spinosa, humilis, folio Aristolochiae, baccis rubris.

Catesby was not cited in the original description (Fl. Carolin. 244. 1788.) Ewan (1974, p. 93) referred this illustration to *Smilax herbacea* L.

Smilax tamnoides L. (**1:** *t. 52*)

Smilax Bryoniae nigrae folijs caule spinoso, baccis nigris.

Linnaeus (Sp. Pl. 1030. 1753) cited only Catesby; however, a specimen obtained by Kalm (LINN 1132.10) is preferable as a lectotype. Ewan (1974, p. 93) referred this illustration to *Smilax bona-nox* L. (H.S. 232, f. 31; OXF-DB; OXF-S.)

ANGIOSPERMAE – DICOTYLEDONEAE

ACERACEAE

Acer rubrum L. (**1:** *t. 62*)

Acer Virginianum, folio majore, subtus argenteo, suprà viridi splendente. Red flowring Maple.

Linnaeus (Sp. Pl. 1055. 1753) cited Catesby, Hortus Upsal., Gronovius, and others. (H.S. 212, f. 14; 232, f. 32.)

ANACARDIACEAE

Anacardium occidentale L. (**2**(App.): *t. 9*)

Pomifera, seu potius prunifera Indica, nuce viniformi summo pomo innascente, Cajous vel Acajous dicta. Cushew Tree.

Linnaeus (Sp. Pl. 383. 1753) cited Catesby, Hortus Cliffort., and others.

Metopium toxiferum (L.) Krug & Urban (**1:** *t. 40*)

Toxicodendron folijs alatis fructu purpureo Pyri formi sparso. Poison-Wood.

Amyris toxifera L. Syst. Nat. ed. 10. 1000. 1759. Linnaeus cited Catesby and Hortus Cliffort.

Rhus glabra L. (**2**(App.): *t. 4*)

Rhus glabrum Panicula speciosa coccinea.

Linnaeus (Sp. Pl. 265. 1753) cited Gronovius and others, but not Catesby.

ANNONACEAE

Annona glabra L.* (**2:** *t. 64*)

Anona maxima, foliis latis fructu maximo luteo conoïde, cortice glabro.

Linnaeus (Sp. Pl. 537. 1753) cited only Catesby but supplied a new phrase name. No supporting specimens have been located. Dandy (1958, p. 112) stated that the plate was the type.

Annona glabra L. (**2:** *t. 67*)

Anona fructu viridi laevi, Pyri inversi forma.

This illustration has been referred to *Annona palustris* L. (Sp. Pl. ed. 2. 757. 1762). Catesby was not cited, and the species is regarded as a synonym of *Annona glabra* L. (1753). Ewan (1974, p. 97) called this illustration *Annona cherimolia* Miller. No associated specimens have been located to verify the identification either way.

Annona reticulata L. (**2:** *t. 86*)

Anona maxima, foliis oblongis, angustis; fructu maximo luteo conoïde; cortice glabro in areolas angulares distincto.

Linnaeus (Sp. Pl. 537. 1753) cited Catesby, Sloane, and Ray. Fawcett and Rendle (Fl. Jamaica **3:** 198. 1914) designated "Sloane Herb. vii. 94" as the type specimen.

Asimina triloba (L.) Dunal* (**2:** *t. 85*)

Anona fructu lutescente, laevi, scrotum Arietis referente.

Annona triloba L. Sp. Pl. 537. 1753. Only Catesby was cited, although a new phrase name was used. Dandy (1958, p. 112) stated that the plate is the type.

APOCYNACEAE

Echites umbellata Jacq. (**1:** *t. 58, below*)

Apocynum Scandens folio, cordato flore albo. Dogs-bane.

Tabernaemontana echites L. Syst. Nat. ed. 10. 945. 1759. Only Sloane was cited.

Plumeria obtusa L.* (**2:** *t. 93, above*)

Plumeria flore niveo, foliis brevioribus obtusis.

Linnaeus (Sp. Pl. 209. 1753) cited only Catesby. Dandy (1958, p. 112) stated that the plate is the type.

Plumeria rubra L. (**2:** *t. 92*)

Plumieria Flore Roseo odoratissimo.

Linnaeus (Sp. Pl. 209. 1753) cited Catesby, Hortus Cliffort., and others.

Urechites lutea (L.) Britton* (**2:** *t. 53*)

Apocynum Scandens, Salicis folio, flore amplo pleno.

Vinca lutea L. Cent. II. Pl. 12. 1756. Dandy (1958, p. 112) called the plate the type. *Echites catesbaei* G. Don (Gen. Syst. **4:** 74. 1838), now regarded as a synonym of *Urechites lutea*, is also based on Catesby's plate.

AQUIFOLIACEAE

Ilex cassine L. (**1:** *t. 31*)

Agrifolium Carolinense folijs dentatis baccis rubris. Dahoon Holly.

Linnaeus (Sp. Pl. 125. 1753) cited Catesby and Hortus Cliffort. (H.S. 212, f. 65. (upper left).)

Ilex vomitoria Aiton (**2:** *t. 57*)

Cassena vera Floridanorum, Arbuscula baccifera Alaternifacie, foliis alternatim sitis, tetrapyrene.

Ilex cassine var. β, L. Sp. Pl. 125. 1753. The variety remains unnamed, and Linnaeus cited Catesby and Plukenet. The type of Aiton's taxon (Hortus Kew. **1:** 170. 1789) is presumably a cultivated plant. Rehder (Jour. Arnold Arb. **3:** 212–215. 1922) discussed the fact that the older name, *Cassine Paragua* Miller (Gard. Dict. ed. 8. no. 2. 1768), based on Catesby's plate, may be considered a later homonym of *Cassine Peragua* L. (Sp. Pl. 268. 1753).

ARALIACEAE

Panax quinquefolius L. (**2**(App.): *t. 16*)

Aureliana Canadensis R. P. Lafiteau. Ginseng.

Linnaeus (Sp. Pl. 1058. 1753) cited Catesby, Gronovius, and others.

ARISTOLOCHIACEAE

Aristolochia serpentaria L. (**1:** *t. 29*)

Aristolochia pistolochia seu Serpentaria Virginiana caule nodoso. Snake-Root of Virginia.

Linnaeus (Sp. Pl. 961. 1753) cited Catesby and Gronovius.

BERBERIDACEAE

Podophyllum peltatum L. (**1:** *t. 24*)

Anapodophyllon Canadense Morini. May Apple.

Linnaeus (Sp. Pl. 505. 1753) cited Catesby, Hortus Cliffort., and Hortus Upsal. (H.S. 212, f. 63 (upper left).)

BIGNONIACEAE

Bignonia capreolata L. (**2:** *t. 82*)

Bignonia Americana, capreolis donata, siliqua breviore.

In the original description (Sp. Pl. 624. 1753) Linnaeus cited Hortus Cliffort., p. 317, but not Catesby. Further discussion was presented by Sprague (Jour. Bot. London **60:** 236–238. 1922). Wilbur (Taxon **29:** 299–303. 1980) has proposed conserving *Bignonia capreolata* L. as the lectotype of the genus *Bignonia* L.

Campsis radicans (L.) Seem. (**1:** *t. 65*)

Bignonia, Fraxini folijs, coccineo flore minore. Trumpet-Flower.

Bignonia radicans L. var. β, L. Sp. Pl. 625. 1753. Only Catesby was cited. Dandy (1958, p. 112) stated that the plate is the type of *Bignonia radicans* var. β. The unnamed variety was not recognized by Rehder (Bibliogr. Cult. Trees Shrubs, 1949). The color variation in various copies of the *Natural History* suggests that the variety is not worthy of recognition.

Catalpa bignonioides Walter (**1:** *t. 49*)

Bignonia Urucu folijs flore sordidé albo, intus maculis purpureijs & luteis asperso, siliqua longissima & angustissima. Catalpa Tree.

Bignonia catalpa L. Sp. Pl. 622. 1753. Catesby and Hortus Cliffort. were cited. (H.S. 212, f. 61; 232, f. 51.)

Jacaranda caerulea (L.) Griseb.* (**1:** *t. 42*)

Arbor Guajaci latiore folio, Bignoniae flore caeruleo, fructu duro in duas partes disiliente, seminibus alatis imbricatim positis. Broad leaf'd Guaicum, with blew Flowers.

Bignonia caerulea L. Sp. Pl. 625. 1753. Only Catesby was cited. Dandy (1958, p. 112) stated that the plate is the type, and H.S. 232, f. 12 (upper right) is the typotype specimen.

Tabebuia bahamensis (Northrop) Britton (**1:** *t. 37*)

Bignonia arbor pentaphylla flore roseo majore siliquis planis. Bignonia.

For *Bignonia pentaphylla* L. (Sp. Pl. ed. 2. 870. 1763) Linnaeus cited Catesby and others. This illustration is not *Tabebuia pentaphylla* (Juss.) Hemsley. (H.S. 232, f. 45 (lower right).)

BORAGINACEAE

Bourreria ovata Miers (**2:** *t. 79*)

Pittoniae similis, Laureolae foliis, floribus albis, baccis rubris.

In the protologue of *Ehretia bourreria* L. (Sp. Pl. ed. 2. 275. 1762), Linnaeus cited Catesby, Browne, Sloane, and others. In 1869 Miers (Ann. Mag. Nat. Hist. IV. **3:** 207) cited Catesby "ii. tab. 79" in his description of the new species *Bourreria havanensis* Miers. In 1911 O. E. Schulz (*in* Urban, Symb.

Antill. 7: 60) excluded the Catesby citation when he referred *B. havanensis* Miers to the synonymy of *Beureria succulenta* var. *revoluta* (Kunth) Schulz. Schulz (*op. cit.*, p. 55) referred Catesby's illustration to *Beureria ovata* Miers, although it was not included in the original description of that species. (H.S. 232, f. 45 (upper right).)

Cordia sebestena L. (**2:** *t. 91, above*)

Caryophyllus spurius inodorus, Folio subrotundo scabro, flore racemoso hexapetaloïde coccineo speciosissimo.

Linnaeus (Sp. Pl. 190. 1753) cited Catesby, Sloane, Dillenius, and Ray. (H.S. 232, f. 24, f. 33.)

BURSERACEAE

Bursera simaruba (L.) Sarg. (**1:** *t. 30*)

Teribinthus major Betulae cortice, fructu triangulari. Gum-elimy Tree.

Pistacia simaruba L. Sp. Pl. 1026. 1753. Linnaeus cited Sloane and Catesby. Fawcett and Rendle (Fl. Jamaica **4**(2): 206. 1920) stated, "Type in Herb. Sloane in Herb. Brit. Mus." Ewan (1974, p. 92) cited this plant under the synonymous name *Elaphrium simaruba* (L.) Rose.

CALYCANTHACEAE

Calycanthus floridus L. (**1:** *t. 46*)

Frutex corni folijs conjugatis, floribus instar Anemones stellatae, petalis crassis, rigidis, colore sordidè rubente; cortice aromatico.

Linnaeus (Syst. Nat. ed. 10. 1066. 1759) cited Catesby, Ehret, Duhamel, and Miller. A lectotype has not been chosen. (H.S. 212, f. 16; BM-Dale.)

CANELLACEAE

Canella winterana (L.) Gaertner (**2:** *t. 50*)

Arbor baccifera, laurifolia, aromatica, fructu viridi calyculato racemoso. Winter's Bark.

Laurus winterana L. (Sp. Pl. 371. 1753). Linnaeus cited Catesby, Hortus Cliffort., and Sloane.

CARYOPHYLLACEAE

Silene virginica L. (**2:** *t. 54*)

Lychnis viscosa, Virginiana, flore amplo coccineo: seu Muscipula Regia.

Linnaeus (Sp. Pl. 419. 1753) cited only Gronovius. Specimens collected by Kalm and Pursh are in the Linnean herbarium. (H.S. 212, f. 18.)

CHRYSOBALANACEAE

Chrysobalanus icaco L. (**1:** *t. 25*)

Frutex cotini fere folio crasso, in summitate deliquium patiente, fructu ovali coeruleo ossiculum angulosum continente. Cocoa Plum.

Linnaeus (Sp. Pl. 513. 1753) did not cite Catesby. Prance (Fl. Neotrop. **9:** 15, 16. 1972) stated that the type was LINN 641.1.

CLETHRACEAE

Clethra alnifolia L. (**1:** *t. 66*)

Alni folia Americana serrata, floribus pentapetalis albis, in spicam dispositis.

Linnaeus (Sp. Pl. 176. 1753) cited Catesby and Gronovius. (H.S. 212, f. 50; 232, f. 35.)

CLUSIACEAE

Clusia rosea Jacq. (**2:** *t. 99*)

Cenchramidea Arbor saxis adnascens, obrotundo pingui folio; fructu pomiformi, in plurimas capsulas granula ficulnea, stilo columnari octogono praeduro adhaerentia continentes, diviso; Balsamum *fundens.* Balsam-Tree.

Linnaeus (Sp. Pl. ed. 2. 1493. 1763) cited Jacquin and Catesby. (H.S. 232, f. 8 (one leaf).)

COMBRETACEAE

Conocarpus erectus L. (**2:** *t. 33, above*)

Manghala arbor Curassavica, foliis Salignis. Button-Wood.

Linnaeus (Sp. Pl. 176. 1753) cited Hortus Cliffort., Sloane, and others, but not Catesby. (H.S. 232, f. 24.)

Laguncularia racemosa (L.) Gaertner (**1:** *t. 86*)

An Thymelaea foliis obtusis.

Conocarpus racemosus L. Syst. Nat. ed. 10. 930. 1759. Linnaeus did not cite Catesby. Britton and Millspaugh (1920, p. 646) were unable to identify this illustration. Although the plant described and illustrated by Catesby has alternate leaves, in all other characters it is clearly the white mangrove of the Bahamas.

COMPOSITAE

Borrichia arborescens (L.) DC. (**1:** *t. 93*)

Chrysanthemum Bermudense Leucoji foliis virentibus crassis.

Buphthalmum frutescens L. Syst. Nat. ed. 10. 1227. 1759. Linnaeus cited only Plumier.

Echinacea purpurea (L.) Moench (**2:** *t. 59*)

Chrysanthemum Americanum, Doronici folio, flore Persici coloris, umbone magno prominente ex atro purpureo, viridi, & aureo fulgente.

Rudbeckia purpurea L. Sp. Pl. 907. 1753. Linnaeus cited Catesby, Gronovius, and others.

Salmea petrobioides Griseb. (**1:** *t. 72*)

Arbor maritima, foliis conjugatis pyriformibus apice in summitate instructis, floribus racemosis luteis.

The type of the Grisebach species is a collection by Swainson from the Bahamas. Catesby incorrectly described and illustrated the florets as yellow instead of white.

Wedelia bahamensis (Britton) O. E. Schulz (**1:** *t. 92*)

Although this plant is illustrated, there is no accompanying text. "*Chrysanthemum &c.*" appears on the plate in the lower right corner. The type of the basionym *Stemmodontia bahamensis* Britton is *Britton and Brace 302,* from the Bahamas. Catesby's plate was cited by Britton and Millspaugh (1920, p. 451).

CONVOLVULACEAE

Ipomoea batatas (L.) Lam. (**2:** *t. 60*)

Convolvulus Radice tuberoso esculento. Virginian Potato.

Convolvulus batatas L. Sp. Pl. 154. 1753. Linnaeus cited Catesby, Hortus Cliffort., and others.

Ipomoea carolina L.* (**2:** *t. 91, below*)

Convolvulus minor Pentaphyllos, flore purpureo minore.

Linnaeus (Sp. Pl. 160. 1753) cited only Catesby. Dandy (1958, p. 112) stated that the plate is the type. (BM-Dale.)

Ipomoea microdactyla Griseb. (**2:** *t. 87, below*)

Convolvulus foliis variis, inferioribus trifariim divisis, superioribus sagittatis; floribus ex rubro purpureis.

Ipomoea sagittata Poiret (**1:** *t. 35*)

Convolvulus Caroliniensis angusto sagittato folio, flore amplissimo purpureo, radice crassa. Purple Bind-weed of Carolina. (OXF-DB.)

CORNACEAE

Cornus florida L. forma **rubra** (Weston) Schelle (**1:** *t. 27*)

Cornus mas Virginiana, flosculis in corymbo digestis perianthio tetrapetalo albo radiatim cinctis. Dogwood Tree.

Linnaeus (Sp. Pl. 117. 1753) cited Catesby, Gronovius, Hortus Cliffort., and Hortus Upsal. (H.S. 212, f. 5 (upper left, buds only); 233, f. 89 (buds); BM-Dale.)

EBENACEAE

Diospyros virginiana L. (**2:** *t. 76*)

Guajacana.

Linnaeus (Sp. Pl. 1057. 1753) cited Catesby, Gronovius, and Hortus Cliffort.

ERICACEAE

Kalmia angustifolia L. (**2**(App.): *t. 17, left*)

Chamaedaphne semper virens, foliis oblongis angustis, foliorum fasciculis oppositis è foliorum alis.

Linnaeus (Sp. Pl. 391. 1753) cited Catesby, Gronovius, and Plukenet.

Kalmia latifolia L. (**2:** *t. 98*)

Chamaedaphne foliis Tini, floribus bullatis umbellatis.

Linnaeus (Sp. Pl. 391. 1753) cited Catesby, Gronovius, and Plukenet. (H.S. 212, f. 64 (lower right, flowers); 232, f. 54 (fruit).)

Leucothoë racemosa (L.) A. Gray (**2:** *t. 43*)

Frutex foliis serratis, floribus longioribus spicatis subviridibus, capsula pentagona.

Linnaeus (Sp. Pl. 394. 1753) cited Catesby and others in the protologue of *Andromeda paniculata* L. Rehder cited "*Andromeda paniculata* L. p.p. max." in the synonymy of *Leucothoë racemosa.* The type of *Andromeda racemosa* L. (Sp. Pl. 394. 1753), the basionym, is a specimen collected by Kalm (LINN 563.15).

Oxydendrum arboreum (L.) DC.* (**1:** *t. 71*)

Frutex folijs oblongis acuminatis, floribus spicatis unoversu dispositis. Sorrel-Tree.

Andromeda arborea L. Sp. Pl. 394. 1753. Linnaeus cited Catesby and "Gronovius virg. 48." The latter reference is to Catesby, and the illustration may well be the type. (H.S. 212, f. 60; 232, f. 57; BM-Dale. No material is in the Linnean herbarium.)

Rhododendron maximum L. (**2**(App.): *t. 17, right*)

Chamaerhododendros lauri-folio semper virens, floribus bullatis corymbosis.

Linnaeus (Sp. Pl. 392. 1753) cited Catesby and "Amoen. Acad. 2. p. 201."

Rhododendron viscosum (L.) Torrey var. **aemulans** Rehder (**1:** *t. 57*)

Cistus Virginiana, flore & odore Periclymeni. Upright Honysuckle.

Azalea viscosa L. (Sp. Pl. 151. 1753). Linnaeus cited Catesby, Gronovius, and others. A specimen collected by Kalm is in the Linnean herbarium.

EUPHORBIACEAE

Croton eluteria (L.) Sw.* (**2:** *t. 46*)

An Ricinoides Aeleagni folio? Ilathera Bark.

Linnaeus (Sp. Pl. 1042. 1753) ended his description of *Clutia cascarilla* L. with a dagger symbol, suggesting an imperfectly known species or some doubt or uncertainty; he cited only Catesby. Dandy (1958, p. 112) stated that the plate was the type. Millspaugh (Publ. Field Mus. Bot. **2:** 306–308. 1909) concluded that this was the same as *Clutia eluteria* L., for which Linnaeus (Sp. Pl. 1042. 1753) cited Hortus Cliffort. and others. Millspaugh combined the taxa on the basis of page priority and accepted the name *Croton eluteria* (L.) Sw. In reaching this conclusion, he also noted the inaccuracy of Catesby's drawing and the fact that Linnaeus later (Sp. Pl. ed. 2. 1424. 1763) changed the description of *Clutia cascarilla* to apply to a taxon known as *Croton linearis* Jacq. Ewan (1974, p. 96) accepted *Croton eluteria* (L.) Sw. for Catesby's plate and stated that the typotype was "H.S. 232, f. 24 [upper left]."

Hippomane mancinella L. (**2:** *t. 95, above*)

Mancanilla Pyri facie. Mancaneel-Tree.

Linnaeus (Sp. Pl. 1191. 1753) cited Catesby, Hortus Cliffort., Sloane, and others. (H.S. 232, f. 5, f. 7.)

Phyllanthus epiphyllanthus L. (**2:** *t. 26*)

Phylanthos Americana Planta flores ad foliorum crenas proferans.

Linnaeus (Sp. Pl. 981. 1753) cited Catesby, Hortus Cliffort., and others. Webster (Jour. Arnold Arb. **39:** 109. 1958) stated that the type was Hortus Cliffort. 439.1 (BM). Ewan (1974, p. 96) used the synonymous name *Xylophylla epiphyllanthus* (L.) Britton for this illustration.

Picrodendron baccatum (L.) Krug & Urban (**2:** *t. 32*)

Tapia trifolia fructu majore oblongo.

Juglans baccata L. Syst. Nat. ed. 10. 1272. 1759. Linnaeus cited "Brown jam. 346. n. 2." Ewan (1974, p. 96) suggested the synonymous name *Picrodendron macrocarpum* (Rich.) Britton.

FAGACEAE

Castanea pumila (L.) Miller (**1:** *t. 9*)

Castanea pumila Virginiana, fructu racemato parvo in singulis capsulis echinatis unico. Chinkapin.

Fagus pumila L. Sp. Pl. 998. 1753. Linnaeus cited Catesby, Gronovius, and others, indicating with an asterisk that a good description was in Gronovius.

Quercus alba L. (**1:** *t. 21, left*)

Quercus alba Virginiana. White Oak.

Linnaeus (Sp. Pl. 996. 1753) cited Catesby and Gronovius.

Quercus incana Bartram (**1:** *t. 22*)

Quercus humilior salicis folio breviore. Highland Willow Oak.

Dandy (1958, p. 112) stated that the plate is the type of *Quercus phellos* L., with a typotype specimen H.S. 212, f. 78. However, Linnaeus cited only Catesby's *t. 22* for his *Quercus phellos* var. γ (Sp. Pl. 994. 1753). Michaux (Hist. Chênes Am. 8. *t. 14.* 1801) cited Catesby when he described *Quercus cinerea* Michx. Sargent (Silva **8:** 172. 1895) raised an earlier variety to specific level as *Quercus brevifolia* Sarg., noting that it was first illustrated and described by Catesby. Bartram's name (Travels N. S. Carolina, 378. 1791) is the oldest and is currently accepted in many floras but does not appear to have been typified.

Quercus laevis Walter (**1:** *t. 23*)

Quercus Esculi divisura foliis amplioribus aculeatis. Red Oak.

The Catesby reference and others were cited by Linnaeus under his *Quercus rubra* L. (Sp. Pl. 996. 1753). The plate is also the type of *Quercus catesbaei* Michx. (Hist. Chênes Am. 17. *tt. 29, 30.* 1801), now considered a synonym of *Q. laevis* Walter (Fl. Carolin. 234. 1788), for which no specimen or reference was cited in the original description. Ewan (1974, p. 92) identified the illustration as *Quercus rubra* L.

Quercus marilandica Muenchh.* (**1:** *t. 19*)

Quercus (forte) Marilandica, folio trifido ad Sassafras accedente. Black Oak.

Linnaeus (Sp. Pl. 996. 1753) cited only Catesby under his *Quercus nigra* L. var. β. Dandy (1958, p. 112) stated that the plate is the type of *Quercus* *nigra* L. var. β, with the typotype H.S. 232, f. 93. Muenchhausen (Hausvater **5:** 252. 1770) cited only Catesby's plate.

Quercus nigra L. (**1:** *t. 20, above*)

Quercus folio non serrato, in summitate quasi triangulo. Water-Oak.

Linnaeus (Sp. Pl. 995. 1753) cited Catesby and Gronovius.

Quercus phellos L. (**1:** *t. 16*)

Quercus, An potius Ilex Marilandica folio longo angusto salicis? Willow oak.

Linnaeus (Sp. Pl. 994. 1753) cited Catesby, Gronovius, and Ray for the typical variety. (H.S. 212, f. 77 (upper); 232, f. 98.)

Quercus prinus L. (**1:** *t. 18*)

Quercus castaneae foliis, procera arbor virginiana. Chesnut-Oak.

Linnaeus (Sp. Pl. 995. 1753) cited Catesby, Hortus Cliffort., Gronovius, and others. A Hortus Cliffort. specimen is in the Linnean herbarium. (H.S. 232, f. 14.)

Quercus rubra L. (**1:** *t. 21, right*)

Quercus Caroliniensis virentibus venis muricata. White Oak, with pointed Notches.

Linnaeus (Sp. Pl. 996. 1753) cited Catesby, Hortus Cliffort., and others for *Quercus rubra* var. β. (H.S. 212, f. 5 (right).)

Quercus virginiana Miller (**1:** *t. 17*)

Quercus sempervirens, foliis oblongis non sinuatis. Live-Oak.

For *Quercus phellos* var. β, Linnaeus (Sp. Pl. 994. 1753) cited only Catesby. Dandy (1958) stated that the plate is the type, with the typotype H.S. 212, f. 81 (lower). Trelease (Mem. Natl. Acad. Sci. **20:** 157. *t. 8.* 1924) referred this variety to the synonymy of *Quercus virginiana.*

FLACOURTIACEAE

Banara minutiflora (A. Rich.) Sleumer (**2:** *t. 42, right*)

Frutex foliis oblongis serratis alternis, Acaciae floribus luteis, fructu brevi, calyculato viridi.

Britton and Millspaugh (1920, p. 284) and Ewan (1974, p. 96) referred Catesby's illustration to *Banara reticulata* Griseb. (1860). Sleumer (Fl. Neotrop. **22:** 88. 1980) proposed the new combination based on the older (1845) *Ilex minutiflora* A. Rich.

GENTIANACEAE

Gentiana catesbaei Walter (**1:** *t. 70*)

Gentiana Virginiana, Saponariae folio, flore coeruleo longiore.

For *Gentiana saponaria* L. (Sp. Pl. 228. 1753) Linnaeus cited Catesby, Gronovius, and Morison. We are unable to find any information on the typification of this name, although a specimen collected by Kalm is in the Linnean herbarium. Catesby's illustration appears to have the partially opened flowers of *G. saponaria* but was identified as *G. catesbaei* Walter by Ewan (1974, p. 94). Fernald (Rhodora **49:** 175, 176. 1947) recognized *G. catesbaei* Walter after that name had been in the synonymy of *G. saponaria* L. for many years. Fernald saw a specimen in Walter's herbarium, which he illustrated. He commented: "Although Walter did not cite Catesby's plate, his intent in giving the name of *G. Catesbaei* is pretty obvious." Fernald quoted Curtis (Boston Jour. Nat. Hist. **1**: 128. 1835) as having said "Tab. 70 of Catesby's Carolina, represents it" and concluded, "There should be no question about the identity of *G. Catesbaei.*" A possible typotype specimen, H.S. 212, f. 87 (lower right), was not dissected, rendering impossible the use of corolla characters given in local floras.

GOODENIACEAE

Scaevola plumieri (L.) Vahl* (**1**: *t. 79*)

Lobelia frutescens, Portulacae folio.

Lobelia plumierii L. Sp. Pl. 929. 1753. Linnaeus cited "Fl. Zey. 313, Plum. gen. 21," and Catesby. Jeffrey (Kew Bull. **34**: 543. 1980) designated Catesby's plate as the lectotype.

HAMAMELIDACEAE

Hamamelis virginiana L. (2(App.): *t. 2*)

Hamamelis.

Linnaeus (Sp. Pl. 124. 1753) cited Catesby, Gronovius, and others. A specimen collected by Kalm is in the Linnean herbarium. (H.S. 212, f. 4 (right).)

Liquidambar styraciflua L. (**2**: *t. 65*)

Liquid-ambari Arbor, seu Styraciflua, Aceris folio, fructu Tribuloïde, i.e. Pericarpio orbiculari ex quam plurimis apicibus coagmentato, semen recondens. Sweet Gum-Tree.

Linnaeus (Sp. Pl. 99. 1753) cited Catesby, Gronovius, Hortus Cliffort., Hortus Upsal., and others. A specimen collected by Kalm is in the Linnean herbarium. (H.S. 212, f. 79; 232, f. 34; BM-Dale.)

JUGLANDACEAE

Carya alba (L.) K. Koch (**1**: *t. 38*)

Nux Juglans alba Virginiensis. Hiccory Tree.

Following Rehder's proposal (Jour. Arnold Arb. **26**: 483. 1945) to consider *Carya alba* L. a *nomen ambiguum,* this species has generally been known as *Carya tomentosa* (Poiret) Nutt. As Rehder indicated, Linnaeus had two taxa in the original description of *Juglans alba* (Sp. Pl. 997. 1753), in which Catesby, Gronovius, and Plukenet were cited. However, Crantz (Inst. Rei Herb. **1**: 157. 1766) listed only Catesby in his description of *Juglans alba,* thus typifying the Linnaean name by excluding the Plukenet and Gronovius references. Ewan (1974, p. 93) identified the figure as *C. tomentosa* (Poiret) Nutt. and stated "This identification applies to the fruit but the leaves are those of *Carya glabra* Mill. according to Dr. Donald E. Stone who says 'if one added trichomes to the drawing of the shoot it would pass for mockernut. *C. tomentosa* is what George Edwards must have been referring to as *Juglans* *alba* L.'" This unresolved problem we leave to specialists, who should examine a possible supporting specimen, H.S. 212, f. 3.

Carya cordiformis (Wangenh.) K. Koch (**1:** *t. 38*, smaller fruit)

Nux Juglans Carolinensis fructu minimo putamine levi. Pignut.

Ewan (1974, p. 93) identified this illustration, stating, "The description of the fruit fits this species according to Dr. Stone."

Juglans nigra L. (**1:** *t. 67*)

Nux juglans nigra Virginiensis. Black Walnut.

Linnaeus (Sp. Pl. 997. 1753) cited Catesby and Hortus Cliffort. (H.S. 232, f. 94, f. 97.)

LAURACEAE

Ocotea coriacea (Sw.) Britton (**2:** *t. 28, above*)

Cornus, foliis Salicis Laureae acuminatis; floribus albis; fructu Sassafras.

Laurus coriacea Sw. (Prodr. 65. 1788) was based on material from Jamaica but occurs in the Bahamas (probably the source of Catesby's material). Catesby's plate is the type of *Laurus catesbyana* Michx. (Fl. Bor. Am. **1:** 244. 1803), transferred by Sargent to *Ocotea* (Silva N. Am. **7:** 11. 1895) and later to *Nectandra* (Garden Forest **2:** 448. 1899), and now considered to be a synonym of *Ocotea coriacea* (Sw.) Britton.

Persea borbonia (L.) Sprengel* (**1:** *t. 63*)

Laurus Carolinensis, folijs acuminatis, baccis caeruleis, pediculis longis rubris insidentibus. Red Bay.

Laurus borbonia L. Sp. Pl. 370. 1753. Linnaeus cited Catesby, Hortus Cliffort., and Gronovius. Catesby's plate was designated the lectotype by Kopp (Mem. N. Y. Bot. Gard. **14:** 44. 1966). (H.S. 212, f. 1.)

Sassafras albidum (Nutt.) Nees var. **molle** (Raf.) Fern. (**1:** *t. 55*)

Cornus mas odorata, folio trifido margine plano, Sassafras dicta.

Laurus sassafras L. Sp. Pl. 371. 1753. Linnaeus cited Catesby, Hortus Cliffort., and others. (BM-Dale.)

LEGUMINOSAE

Acacia tortuosa (L.) Willd. (**2:** *t. 44*)

Arbor foliis pinnatis, spica pendula sericea.

Mimosa tortuosa L. Sp. Pl. ed. 2. 1505. 1763. The type is a specimen collected by Browne in Jamaica (LINN 1228.27).

Caesalpinia bahamensis Lam. (**2:** *t. 51, above*)

Pseudo-Santalum croceum. Brasiletto.

Linnaeus (Sp. Pl. 380. 1753) cited Catesby, Plumier, Ray, and Sloane in the protologue of *Caesalpinia brasiliensis.* Urban (Symb. Antill. **2:** 286. 1900) noted that three species were involved, one being "*Caesalpinia bahamensis* Lam. (ex Catesb. Car. t. 51. cum patria erronea Carolina)." Lamarck (Encycl. Méth. Bot. **1:** 461. 1785) had cited Miller, Sloane, and Catesby. *Caesalpinia brasiliensis* L. is typified by a Plumier reference and is endemic to Hispaniola. The Sloane description given by Linnaeus is *Peltophorum brasiliense* Urban (Symb. Antill. **2:** 286. 1900), which was proposed as a combination with the basionym *Caesalpinia brasiliense* Sw. (not L.) (Obs. Bot. 166. 1791) but should be considered a new name credited to Urban. Fawcett & Rendle (Fl. Jam. **4:** 90. 1920) referred to a Browne specimen named by Linnaeus in the Linnean herbarium; however, either the Sloane reference (Voy. Is. Nat. Hist. II, 184. *t. 231, figs. 3, 4*) or the supporting specimen (if located) is more appropriate for typification.

Dalbergia ecastophyllum (L.) Taub. (**2:** *t. 24*)

Arbor, Populi nigrae foliis; fructu reni-formi mono-spermo.

Hedysarum ecastophyllum L. Syst. Nat. ed. 10. 1169. 1759. Ewan (1974, p. 95) identified this illustration as *Ecastophyllum brownei* Pers., which is distinguished on the basis of several characters that cannot be determined from Catesby's description or illustration. No supporting specimen has been located, and the problem is unresolved.

Erythrina herbacea L. (**2:** *t. 49*)

Corallodendron humile, spica florum longissima coccinea, radice crassissimo.

Linnaeus (Sp. Pl. 706. 1753) cited Catesby (*t. 49*), Royen, Dillenius (*t. 90*), and Hortus Cliffort., with references to Carolina and "Missipi." Krukoff (Brittonia **3:** 284. 1939) cited Catesby and stated the type location to be Carolina. He noted that the specimens in the Linnean herbarium appeared in 1767 and therefore cannot be the type. "The description, the plates cited by Linnaeus and the fact that only one species of *Erythrina* is found in Carolina provide sufficient evidence for interpretation of the species" (Krukoff, *loc. cit.*).

Galactia rudolphioides (Griseb.) Bentham & Hooker (**2:** *t. 28, below*)

An Phaseolus minor lactescens flore purpureo.

Dioclea rudolphioides Griseb. Mem. Am. Acad. II. **8:** 178. 1860. The type is *Wright 1181* from Cuba.

Gleditsia aquatica Marsh. (**1:** *t. 43*)

Acacia Abruae folijs, triacanthos, capsulâ ovali unicum semen claudente. Acacia.

Gleditsia triacanthos var. *β*, L. Sp. Pl. 1057. 1753. Linnaeus cited only Catesby. Marshall (Arbust. Am. 54. 1785) did not cite Catesby in the original description. (H.S. 212, f. 61 (upper).)

Haematoxylon campechianum L. (**2:** *t. 66*)

Lignum campechianum; species quaedum Brasil. Logwood.

Linnaeus (Sp. Pl. 384. 1753) cited Catesby, Hortus Cliffort., and Sloane. The type is LINN 538.1. (H.S. 232, f. 81, f. 90.)

Lysiloma latisiliquum (L.) Bentham (**2:** *t. 42, left*)

Acacia, Buxi foliis rotundioribus, floribus albis, siliqua lata compressa.

The discussions of Gillis and Stearn (Taxon **23:** 185–191. 1974), De Wit (Taxon **24:** 349–352. 1975), and Polhill and Stearn (Taxon **25:** 323. 1976) are pertinent, although Linnaeus did not cite Catesby.

Pithecellobium bahamense Northrop (**2:** *t. 97*)

Acacia foliis amplioribus; siliquis cincinnatis.

Linnaeus described *Mimosa circinalis* L. (Sp. Pl. 517. 1753) and cited only Plumier (Spec. 17) for a plant from Hispaniola. Later (Sp. Pl. ed. 2. 1500.

1763), he added references to Catesby and Browne. This taxon as *Pithecellobium circinalis* (L.) Bentham is considered endemic to Hispaniola. Britton and Millspaugh (1920, p. 156) referred Catesby's illustration to *Pithecolobium mucronatum* Britton ex Coker, but this species has been considered a synonym of *Pithecellobium bahamense* Northrop in the Corrells' *Flora of the Bahama Archipelago* (1982).

Robinia hispida L. (**2**(App.): *t. 20*)

Pseudo Acacia hispida floribus roseis.

Linnaeus (Mant. Pl. 101. 1767) cited Catesby, Jacquin, and Miller.

LOGANIACEAE

Gelsemium sempervirens (L.) Aiton (**1:** *t. 53*)

Gelseminum sive Jasminum luteum ordoratum Virginianum scandens, semper virens.

Bignonia sempervirens L. Sp. Pl. 623. 1753. Linnaeus cited Catesby, Ray, Royen, and Plukenet.

Spigelia marilandica (L.) L. (corrected reference) (**2:** *t. 78*)

Gentiana forte? quae Periclymeni Virginiani *flore coccineo, Planta* Marilandica *spicata erecta, foliis conjugatis.* Indian Pink.

Lonicera marilandica L. (Syst. Nat. **12:** 166. 1767). No specimens or references were cited. In the same volume (p. 734), Linnaeus transferred the taxon to *Spigelia,* a combination generally overlooked in current floras. There are no specimens in the Linnean herbarium, and a neotype should be designated. (H.S. 212, f. 33 (middle).)

LORANTHACEAE

Dendropemon purpureum (L.) Krug & Urban* (**2:** *t. 95, below*)

Viscum foliis latioribus; baccis purpureis pediculis incidentibus.

Viscum purpureum L. Sp. Pl. 1023. 1753. Linnaeus cited only Catesby. No supporting specimen has been located.

Phoradendron rubrum (L.) Griseb.* (**2:** *t. 81, below*)

Viscum foliis longioribus baccis rubris.

Viscum rubrum L. Sp. Pl. 1023. 1753. Linnaeus cited only Catesby, and Dandy (1958, p. 112) stated that the plate is the type. (H.S. 232, f. 2 (lower right), f. 8 (upper left specimen marked lectotype), f. 16 (upper left).)

MAGNOLIACEAE

Liriodendron tulipifera L. (**1:** *t. 48*)

Arbor Tulipifera Virginiana tripartito aceris folio, media lacinia velut abscissa.

Linnaeus (Sp. Pl. 535. 1753) cited Catesby, Hortus Cliffort., and others. (H.S. 212, f. 80.)

Magnolia acuminata (L.) L.* (**2**(App.): *t. 15*)

Magnolia flore albo, folio majore acuminato haud albicante.

Magnolia virginiana var. ε *acuminata* Sp. Pl. 536. 1753. Catesby and Gronovius are cited.

Magnolia acuminata (L.) L. Syst. Nat. ed. 10. **2:** 1082. 1759. Linnaeus cited Catesby and Kalm. Dandy (1958, p. 112) stated that the plate is the type of *Magnolia acuminata* (L.) L.

Magnolia grandiflora L. (**2:** *t. 61*)

Magnolia altissima, flore ingenti candido. Laurel Tree of Carolina.

Linnaeus (Syst. Nat. ed. 10. 1082. 1759) cited Catesby, Trew, and others.

Magnolia tripetala (L.) L.* (**2:** *t. 80*)

Magnolia, amplissimo flore albo, fructu coccineo. Umbrella Tree.

Magnolia virginiana var. *tripetala* L. Sp. Pl. 536. 1753. Linnaeus cited only Catesby.

Magnolia tripetala (L.) L. Syst. Nat. ed. 10. **2:** 1082. 1759. Linnaeus cited only Catesby, and Dandy (1958, p. 112) stated that the plate is the type.

Ewan (1974, p. 98) referred this illustration to *Magnolia macrophylla* Michx., a species with a very different leaf shape.

Magnolia virginiana L. (**1:** *t. 39*)

Magnolia Lauri folio, subtus albicante. Sweet flowring Bay.

Magnolia virginiana L. var. *glauca* L. Sp. Pl. 535. 1753. Linnaeus cited Catesby, Dillenius, and Plukenet.

Magnolia glauca (L.) L. Syst. Nat. ed. 10. **2:** 1082. 1759. Here Linnaeus cited Trew, Ehret, Catesby, Dillenius, and Plukenet. Dandy (1958, p. 112) stated that the plate is the type of *Magnolia glauca* (L.) L.*

MALVACEAE

Hibiscus tiliaceus L. (**2:** *t. 90*)

Ketmia, amplissimo Tiliae folio, subtus argenteo, Flore magno luteo. Maho-Tree.

Linnaeus (Sp. Pl. 694. 1753) did not cite Catesby. Ewan (1974, p. 99) incorrectly referred this illustration to *Thespesia populnea* (L.) Solander. Fryxell (pers. comm.) recognizes the native western hemisphere plant as *Hibiscus pernambucensis* Arruda. The supporting Catesby specimen, H.S. 232, f. 120 (lower), agrees with the description of this species.

Phymosia abutiloides (L.) Ham. (**1:** *t. 77*)

Ketmia frutescens glauca, Aceris majoris folio longiore, serrato, flore carneo.

Malva abutiloides L. Sp. Pl. ed. 2. 971. 1763. Linnaeus cited only Dillenius, "elth. 1, t. 1, f. 1." (H.S. 232, f. 120 (upper right); BM-Dale.)

MELIACEAE

Swietenia mahagoni (L.) Jacq. (**2:** *t. 81, above*)

Arbor foliis pinnatis, nullo impari Alam claudente, nervo ad latus unum excurrente, fructu anguloso magno, semine alato instar Pinûs. Mahogany Tree.

Cedrela Mahag. L. Syst. Nat. ed. 10. **2:** 940. 1759. Linnaeus cited only Catesby, and Dandy (1958, p. 112) stated that the plate is the type of *Cedrela mahagoni* L. Pennington (*in* Pennington & Styles, Fl. Neotrop. **28:** 401. 1981) agrees.

MENISPERMACEAE

Cocculus carolinus (L.) DC. (**1:** *t. 51*)

Smilax (forte) lenis, folio anguloso hederaceo.

Menispermum carolinum L. Sp. Pl. 340. 1753. Linnaeus cited no references for this taxon, and no plant material on which it was based is still in existence. However, under *Cissampelos smilacina* L. (Sp. Pl. 1032. 1753) Linnaeus cited only Catesby, so the illustration is the type of that specific name. The latter taxon has been of uncertain placement. Asa Gray (Synopt. Fl. N. Am. **1:** 64–66. 1895) cited Catesby's plate and referred *C. smilacina* L. to *Cocculus carolinus* (L.) DC. However, according to both the entry in *Index Kewensis* and Diels (*in* Pflanzenr. IV. **94:** 257. 1910), *C. smilacina* is *Menispermum canadense* L. Ewan (1974, p. 93) stated, "Though *Cocculus carolinus* (L.) DC. occurs in the region visited by Catesby there is little doubt this is *Menispermum* [*canadense* L.]." However, Catesby illustrated and described red fruits (characteristic of *Cocculus*), while *Menispermum canadense* has black fruits. Among possible supporting specimens, H.S. 232, f. 41 and f. 104 are *Cocculus*, but H.S. 212, f. 21 is a *Menispermum*. It would appear that either a neotype should be designated for *Cocculus* (*Menispermum*) *carolinus* or, less desirably, that the name of this well-known species should be changed to utilize the basionym *Cissampelos smilacina*, which is typified by Catesby's plate.

MONOTROPACEAE

Monotropa uniflora L. (**1:** *t. 36*)

Orobanche Virginiana flore pentapetalo cernuo. Broom-rape.

Linnaeus (Sp. Pl. 387. 1753) cited Catesby and Gronovius.

MORACEAE

Ficus citrifolia Miller (**2**(App.): *t. 18*)

Ficus citrii folio, fructu parvo purpureo.

Ficus indica L. var. *β.*, L. Sp. Pl. 1060. 1753. Linnaeus cited Catesby, Hortus Cliffort., Sloane, and others. According to De Wolf (*in* Woodson, Fl. Panama, IV. **2:** 160. 1960), the taxon is typified by "a specimen in Herb. Banks." Ewan (1974, p. 100) identified this illustration as *Ficus brevifolia* Nutt., a name now considered to be a synonym.

MYRICACEAE

Myrica cerifera L. (**1:** *t. 69*)

Myrtus, Brabanticae similis, Carolinensis, baccata, fructu racemoso sessili monopyreno. Narrow-leaved Candle-berry Myrtle.

Linnaeus (Sp. Pl. 1024. 1753) cited Catesby, Hortus Cliffort., Hortus Upsal., Gronovius, and others. (BM-Dale.)

Myrica pensylvanica Loisel (**1:** *t. 13*)

Myrtus Brabanticoe similis Caroliniensis humilior; foliis latioribus & magis Serratis. Broad-leaved Candle-berry Myrtle.

Linnaeus (Sp. Pl. 1024. 1753) cited only Catesby under *M. cerifera* L. var. *β*. Loisel (*in* Duhamel, Traité Arbres Arbustes, ed. augm. **2:** 190. *t. 55.* 1804) cited Catesby but also published a plate. The type is then either Catesby's or Loisel's illustration. (H.S. 232, f. 50.)

NYSSACEAE

Nyssa aquatica L.* (**1:** *t. 60*)

Arbor in aqua nascens, folijs latis acuminatis & dentatis, fructu Eleagni majore. Water-Tupelo.

Linnaeus (Sp. Pl. 1058. 1753) cited Catesby, *tt. 41* and *60,* as well as Hortus Cliffort., Gronovius, and Plukenet. Eyde (Taxon **13:** 131. 1964) discussed the complicated problem. We accept his implication that Catesby's *t. 60* is the best option for the type. Supporting specimens are H.S. 212, f. 67 (left), and 232, f. 52 (right). Ewan (1974, p. 94) has identified this illustration as *Nyssa ogeche* Bartram, a very different plant.

Nyssa sylvatica Marsh. (**1:** *t. 41*)

Arbor in aqua nascens, folijs latis acuminatis & non dentatis fructu Eleagni minore. Tupelo Tree.

As indicated above, Linnaeus (Sp. Pl. 1058. 1753) cited this plate under *Nyssa aquatica.* Eyde (Taxon **13:** 130, 131. 1964) stated, "in the absence of a specimen, Marshall's description is the type." However, Catesby's *t. 41* must be the lectotype—not Marshall's "description." Ewan (1974, p. 93) identified this illustration as *Nyssa aquatica* L.

OLEACEAE

Chionanthus virginicus L. (**1:** *t. 68*)

Amelanchior Virginiana, Lauro cerasifolio. Fringe Tree.

Linnaeus (Sp. Pl. 8. 1753) cited Catesby and Hortus Cliffort.

Fraxinus americana L. (**1:** *t. 80*)

Fraxinus Carolinensis, folijs angustioribus utrinque acuminatis, pendulis.

Linnaeus (Sp. Pl. 1057. 1753) cited Catesby, Gronovius, and Ray. A specimen collected by Gronovius is in the Linnean herbarium. (H.S. 212, f. 11 (lower).)

Osmanthus americanus (L.) Gray (**1:** *t. 61*)

Ligustrum Lauri folio, fructu violaceo. Purple-berried Bay.

Olea americana L. Mant. Pl. 24. 1767. Linnaeus cited only Catesby, but he indicated a specimen from "D. Guarden." Peter Green (Notes Roy. Bot. Gard. Edinburgh **22:** 463. 1958) has designated an unmarked sheet in the Linnean herbarium from Dr. Garden as the type specimen. The combination in *Osmanthus* has been incorrectly attributed to Bentham and Hooker (Gen. Pl. **2:** 677. 1876), who only implied it by listing the species under *Osmanthus.* (H.S. 212, f. 22 (upper).)

PASSIFLORACEAE

Passiflora cuprea L.* (**2:** *t. 93, below*)

Grandilla, foliis Sarsaparillae trinerviis; flore purpureo; fructu Olivaeformi caeruleo.

Linnaeus (Sp. Pl. 955. 1753) cited Amoen. Acad. (**1:** 218. *fig. 2.* 1749), Dillenius, Martens, and Catesby. Theoretically, any of the plates is available for typification. Ewan (1974, p. 99) noted that Catesby's plate is "cited in *Sp. pl.* where three additional references are cited but the 'Habitat' is given only as 'Providentia, Bahama.' and thus fixes the type in the present-day type concept for the Linnaean name." (H.S. 232, f. 22 (lower center).)

Passiflora suberosa L. (**2:** *t. 51, below*)

Flos Passionis minimus, trilobatus flore sub-caeruleo.

Linnaeus (Sp. Pl. 958. 1753) did not cite Catesby. Ewan (1974, p. 97) identified this illustration as *Passiflora pallida* L. and cited Killip (Publ. Field Mus. Bot. **19:** 88–97. 1938), although Killip in that publication accepted *Passiflora suberosa* L. and listed *P. pallida* L. as a synonym. Killip (p. 97) rejected "rules of page priority [that] would require the use of the name *P. pallida*" and noted but did not cite as a type the specimen in the Linnean herbarium that Linnaeus had in 1753. (BM-Dale.)

PLATANACEAE

Platanus occidentalis L. (**1:** *t. 56*)

Platanus Occidentalis. Western Plane Tree.

Linnaeus (Sp. Pl. 999. 1753) cited Catesby and Hortus Cliffort. (H.S. 212, f. 68 (upper).)

POLYGONACEAE

Coccoloba diversifolia Jacq. (**2:** *t. 94*)

Cerasus latiore folio; fructu racemoso purpureo majore. Pigeon-Plum.

In the second edition of *Species Plantarum* (**1:** 677. 1762), Linnaeus cited Catesby's *t. 94,* Gronovius, and Royen in the protologue of *Prunus virginiana* (q.v.), but not Catesby's **1:** *t. 28* or Plukenet as he had done in the first edition.

Coccoloba uvifera (L.) L. (**2:** *t. 96*)

Prunus maritima racemosa, folio rotundo glabro; fructu minore purpureo. Mangrove Grape Tree.

Polygonum uvifera L. Sp. Pl. 365. 1753. Linnaeus cited Catesby and Hortus Cliffort. (H.S. 232, f. 8 (lower right).)

PRIMULACEAE

Dodecatheon meadia L.* (**2**(App.): *t. 1*)

Meadia.

Linnaeus (Sp. Pl. 144. 1753) cited only Catesby and Plukenet (Alm. Bot. 62. *t. 79. fig. 6.* 1696). Dandy (1958, p. 112) stated that the plate is the type, thus designating a lectotype by choosing Catesby and rejecting Plukenet.

RHAMNACEAE

Colubrina elliptica (Sw.) Briz. & Stern (**1:** *t. 10*)

Frutex Lauri folio pendulo, fructu tricocco, semine nigro splendente. Red-Wood.

Ewan (1974, p. 92) identified this illustration as *Colubrina reclinata* (L'Hér.) Brongn., which is now regarded as a synonym of *C. elliptica.*

Reynosia septentrionalis Urban (**1:** *t. 75*)

Prunus Buxi folio cordato, fructu nigro rotundo. Bullet-Bush.

Sargent (Silva N. Am. **2:** 21. *t. 56.* 1891) noted that Catesby's plate was the earliest account of *Reynosia latifolia* Griseb. Urban (Symb. Antill. **1:** 356. 1899) separated the Bahamian and the Cuban plants, although both species are recognized in the current flora of Cuba.

RHIZOPHORACEAE

Rhizophora mangle L. (**2:** *t. 63*)

Candela Americana, foliis Laurinis, flore tetrapetalo luteo, fructu angustiore. Mangrove Tree.

Linnaeus (Sp. Pl. 443. 1753) did not cite Catesby.

ROSACEAE

Prunus virginiana L. (**1:** *t. 28*)

Cerasi similis arbuscula Mariana. Poedi folio, flore albo parvo racemoso. Cluster'd black Cherry.

Linnaeus (Sp. Pl. 473. 1753) cited Catesby's *t. 28,* Gronovius, Royen, and "Pluk. mant. 43. t. 339." He later (Sp. Pl. ed. 2. **1:** 677. 1762) changed the references, adding Catesby **2:** *t. 94* (*Coccoloba diversifolia* Jacq.) and eliminating mention of *t. 28.* (OXF-S.)

RUBIACEAE

Casasia clusiifolia (Jacq.) Urban (**1:** *t. 59*)

Arbor Jasmini, floribus albis, folijs Cenchranmideoe, fructu ovali, seminibus parvis nigris mucilagine involutis. Seven Years Apple.

Catesbaea spinosa L.* (**2:** *t. 100*)

Frutex Spinosus Buxi foliis, plurimis simul nascentibus; flore tetrapetaloide, pendulo, sordide flavo, tubo longissimo; fructu ovali croceo, semina parva continente.

Linnaeus (Sp. Pl. 109. 1753) cited only Catesby. Dandy (1958, p. 112) stated that the type of *C. spinosa* L., H.S. 232, f. 21 (upper left and lower right), is thus the type of the specific and generic names. The generic name is correctly attributed to Linnaeus (Farr *et al.,* Index Nom. Gen. **1:** 303. 1979), although Catesby stated "Catesbaea†. *Lycium* Catesbeii, *Authore* D. Gronovio" and, in a footnote, "It is not without Reluctancy, that I here exhibit a Plant with my own Name annexed to it; but the Regard and Obligations I owe to my learned Friend Dr. J. F. Gronovius of Leyden, who was pleased some Years since to honor me, tho' undeservedly, with the Title of this Genus, obliges me not to suppress it." The binomial "Lycium Catesbeii" has not been located in Gronovius's publications. In addition to the above-mentioned specimens in the Sloane herbarium, there is a better one in the general herbarium at BM from Gronovius.

Mitchella repens L. (**1:** *t. 20, below*)

Myrti subrotundis folijs, floribus albis gemellis ex provincia Floridana. Syringa Baccifera.

Linnaeus (Sp. Pl. 111. 1753) cited Catesby, Gronovius, and others.

RUTACEAE

Amyris elemifera L. (**2:** *t. 33, below*)

Frutex trifolius resinosus; floribus tetra-petalis albis racemosis.

Linnaeus (Syst. Nat. ed. 10. 1000. 1759) cited Catesby and Hortus Cliffort. Fawcett and Rendle (Fl. Jamaica **4:** 191. 1920) suggested that a specimen in the Linnean herbarium collected by Browne was the type.

Ptelea trifoliata L. (**2:** *t. 83*)

Frutex Virginianus trifolius, Ulmi Samaris; Banisteri.

Linnaeus (Sp. Pl. 118. 1753) did not cite Catesby. (H.S. 212, f. 66 (upper left); 232, f. 53.)

Zanthoxylum clava-herculis L. (**1:** *t. 26*)

Zanthoxylum spinosum, Lentisci, longioribus folijs Euonimi fructu capsulari ea Insula Jamaicensi. Pellitory, or Tooth-ach Tree.

Linnaeus (Sp. Pl. 270. 1753) cited Catesby and Hortus Cliffort. in the protologue and gave the distribution as Jamaica, Carolina, and Virginia. We suspect that Catesby's reference to Jamaica is in error. The only associated specimen (BM-Dale) is *Z. clava-herculis. Zanthoxylum clava-herculis* Sw. (Obs. Bot. 375. 1791), not L. (1753), from Jamaica has been referred to the synonymy of *Z. martinicense* DC.

SALICACEAE

Populus heterophylla L. (**1:** *t. 34*)

Populus nigra folio maximo gemmis Balsamum odoratissimum fundentibus. Black Poplar of Carolina.

For *Populus balsamifera* L. (Sp. Pl. 1034. 1753) Linnaeus cited Catesby and Hortus Cliffort. Rouleau (Rhodora **48:** 103–110. 1946) concluded that Catesby illustrated *Populus heterophylla* but described a mixture of *P. heterophylla* and *P. deltoides.* Rouleau cited a specimen in the British Museum, which may have been H.S. 212, f. 11 (upper) or 232, f. 52 (left, 1 leaf).

SAPOTACEAE

Manilkara bahamensis Lam & Meeuse (**2:** *t. 87, above*)

Anona foliis Laurinis, in summitate incisis; fructu compresso scabro fusco, in medio acumine longo. Sappadillo Tree.

For *Sloanea emarginata* L. (Sp. Pl. 512. 1753) Linnaeus cited only Catesby but incorrectly attributed the plant to Carolina. Dandy (1958, p. 112) stated that the plate was the type of *Sloanea emarginata* L.*, with the typotype H.S. 232, f. 15.

Achras bahamensis Baker (*in* J. D. Hooker, Ic. Pl. 18. *t. 1795.* 1888) was typified by *Eggers 3837*, from Fortune Island, and Catesby's plate was cited, but Baker was unaware of Linnaeus's description of the plant in the genus *Sloanea. Manilkara bahamensis* Lam & Meeuse (Blumea **4:** 354. 1941) is therefore to be treated as a new name and not a new combination (Art. 72, Note 1). The Linnaean specific epithet cannot be transferred as *Manilkara emarginata* (L.) Britton & Wilson (Sci. Survey Porto Rico Virgin Is. **6:** 366. 1926) because it would be a later homonym of *M. emarginata* Lam (Bull. Jard. Bot. Buitenzorg, III. **7:** 241. 1925), a plant from the Hawaiian Islands.

Mastichodendron foetidissimum (Jacq.) Lam (**2:** *t. 75*)

Cornus, foliis Laurinis, fructu majore luteo. Mastic Tree.

Ewan (1974, p. 98) suggested *Sideroxylon foetidissimum* Jacq. for this illustration. That name serves as the basionym.

SARRACENIACEAE

Sarracenia × catesbaei (Ell.) Bell* (**2:** *t. 69*)

Sarracena, foliis longioribus & angustioribus; Bucanephyllon elatius Virginianum, &c.

Catesby, Hortus Cliffort., and Gronovius were cited under *Sarracenia flava* L. (Sp. Pl. 510. 1753). Elliot (Sketch Bot. S.-Carolina Georgia **2:** 11. 1824) cited Catesby. Bell (Jour. Elisha Mitchell Sci. Soc. **68:** 60. 1952) discussed the hybrid status suggested for Catesby's plant. (H.S. 212, f. 20, f. 21, f. 45.)

Sarracenia purpurea L. (**2:** *t. 70*)

Sarracena, foliis brevioribus latioribus. Sarracena Canadensis, foliis cavis & auritis.

Linnaeus (Sp. Pl. 510. 1753) cited Catesby, Hortus Cliffort., and Gronovius. (BM-Dale.)

SAXIFRAGACEAE

Philadelphus inodorus L.* (**2:** *t. 84, above*)

Philadelphus flore albo majore inodoro.

Linnaeus (Sp. Pl. 470. 1753) cited only Catesby. Dandy (1958, p. 112) stated that the plate is the type, with the typotype H.S. 212, f. 16 (upper right). (OXF-DB.)

STERCULIACEAE

Theobroma cacao L.* (**2**(App.): *t. 6*)

Cacao Arbor. Cacao Tree.

Linnaeus (Sp. Pl. 782. 1753) cited Catesby, Hortus Cliffort., and others. Cuatrecasas (Contr. U. S. Natl. Herb. **35:** 496. 1964) selected H.S. 5, f. 59 as the lectotype.

STYRACACEAE

Halesia tetraptera Ellis (**1:** *t. 64*)

Frutex, Padi folijs non serratis, floribus monopetalis albis, campani-formibus, fructu crasso tetragono.

Halesia carolina L. (Syst. Nat. ed. 10. 1044. 1759). Linnaeus cited Catesby and material collected by Ellis. Reveal and Seldin (Taxon **25:** 123–140. 1976), discussing in detail the identity of Linnaeus's species, concluded (p. 127) that it was different than the one illustrated by Catesby, and that Linnaeus had based his description of *H. carolina* "only on the material sent to him by Ellis. The Catesby illustration is somewhat difficult to associate with a given species only because it is not entirely accurate. However, it appears to represent the Coastal Plain phase of *Halesia carolina,* sensu authors, which is now infrequently encountered near Charleston. Little can be gleaned from Catesby's rather long description."

SYMPLOCACEAE

Symplocos tinctoria (L.) L'Hér. (**1:** *t. 54*)

Arbor lauri folio, floribus ex foliorum, alis pentapetalis, pluribus staminibus donatis.

Hopea tinctoria L. (Mant. Pl. 105. 1767; Syst. Nat. ed. 12. 509. 1767). The two references are considered to have been published simultaneously. Linnaeus cited Catesby and appears to have credited the genus to Garden but called the illustrated plant "mala." A specimen in the Linnean herbarium (942.1) may be from Dr. Garden and is in fruit. A specimen collected by Catesby and in the Gronovius herbarium (BM) is in flower. Although Linnaeus described both flowers and fruit, we designate the specimen in his herbarium as the lectotype.

THEACEAE

Gordonia lasianthus (L.) Ellis (**1:** *t. 44*)

Alcea Floridana quinque capsularis Laurinis folijs, leviter crenatis, seminibus coniferarum instar alatis. Loblolly Bay.

In the protologue of *Hypericum lasianthus* L. (Sp. Pl. 783. 1753), Linnaeus cited Catesby, Hortus Cliffort., and others. Later, Linnaeus (Mant. Pl. **2:** 570. 1771) used *Gordonia lasianthus* and cited the second edition of *Species Plantarum* (1763, p. 1101). The generic name is attributed to Ellis (Philos. Trans. **60:** 520. 1771) and is conserved (#5148). (H.S. 212, f. 13 (lower); 232, f. 50 (right); BM-Dale; OXF-S.)

Stewartia malacodendron L. (**2**(App.): *t. 13*)

Steuartia.

Linnaeus (Sp. Pl. 698. 1753) cited Catesby and "Act. Ups. 1741, 79, t. 2."

THEOPHRASTACEAE

Jacquinia keyenis Mez (**1:** *t. 98*)

Frutex Buxi foliis oblongis, baccis pallide viridibus apice donatis. Soap-Wood.

Catesby's illustration was cited by Britton and Millspaugh (1920, p. 317).

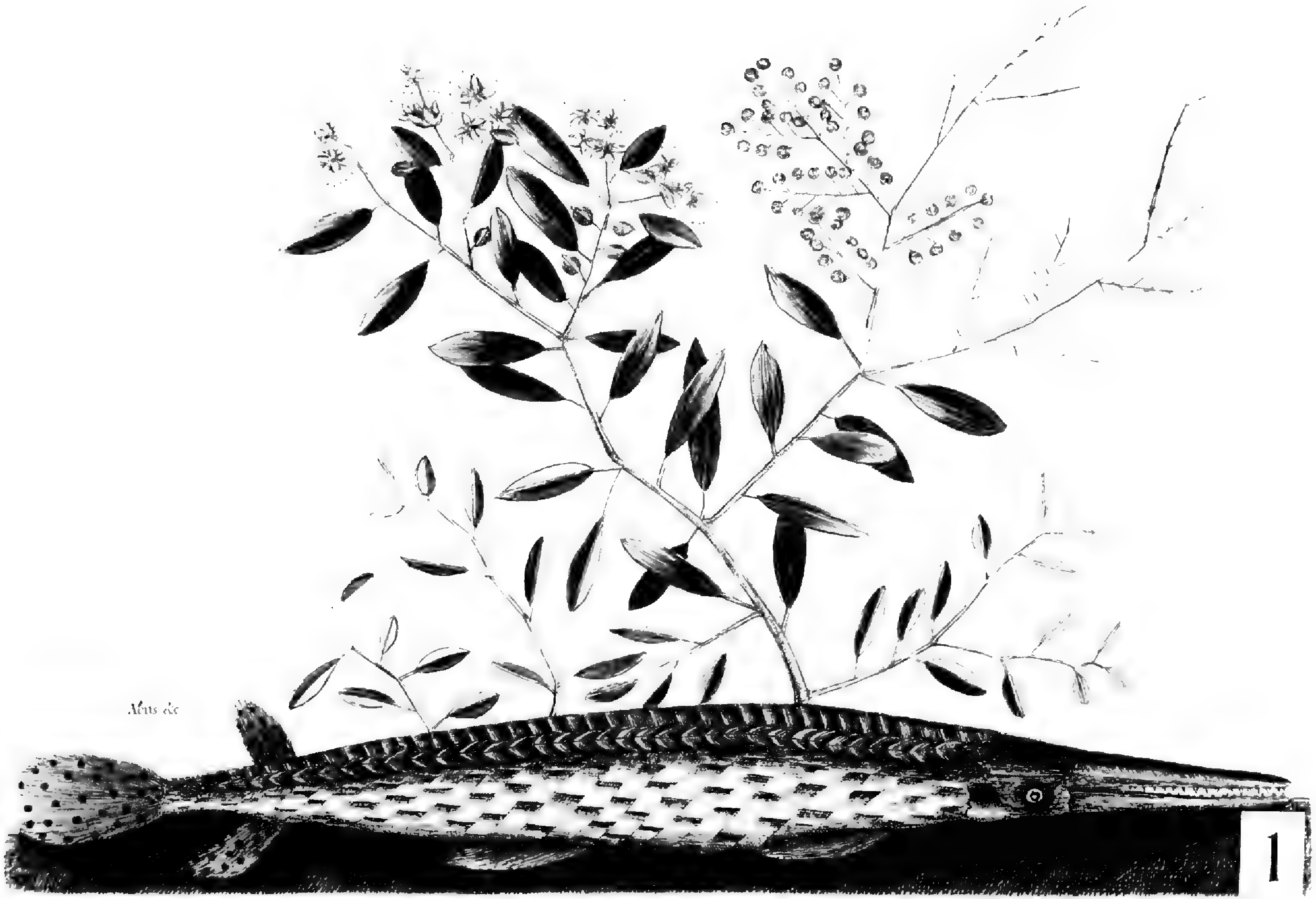

FIGURE 1. Catesby's illustration of "Frutex aquaticus, floribus luteis, fructu rotundo quinque-capsulari" (Vol. 2, *t. 30*). Unidentified.

VERBENACEAE

Avicennia germinans (L.) L. (**1:** *t. 85*)

Frutex Bahamensis foliis oblongis succulentis, fructu subrotundo unicum nucleum continente.

Bontia germinans L. (Syst. Nat. ed. 10. 1122. 1759; Sp. Pl. ed. 2. 891. 1763). LECTOTYPE: *Browne* (LINN 813.2), according to Stearn (Kew Bull. **1958:** 34. 1958). Ewan (1974, p. 95) identified this illustration as *Avicennia nitida* Jacq., a synonymous name.

Callicarpa americana L. (**2:** *t. 47*)

Frutex baccifer, verticillatus; folijs scabris latis dentatis, & conjugatis; baccis purpurijs dense congestis.

Linnaeus (Sp. Pl. 111. 1753) cited Catesby and Gronovius. A specimen collected by Gronovius is LINN 136.1.

VITACEAE

Cissus tuberculata Jacq. (**2:** *t. 48*)

Frutex Rubo similis, non spinosus, capreolatus; fructu racemoso caeruleo Mori-formi.

UNPLACED ILLUSTRATIONS

2: *t. 30, above. Frutex aquaticus, floribus luteis, fructu rotundo quinque-capsulari.*

Edwards and Forster were unable to identify this illustration (see FIGURE 1). Ewan (1974, p. 96) suggested with reservations *Samolus ebracteatus* HBK. (Primulaceae), stating that, "The inflorescence as drawn bears a striking resemblance."

Catesby (**2:** 30) described this plant as follows:

> These Plants grow usually about twelve Feet high, arising with innumerable small Stems, alternately bent, from which shoots forth smaller Twigs, set with small pointed smooth Leaves; the Flowers grow on the Tops of the Branches before they open, being inclosed in small brown pointed *Periantheums,* set on short Foot-stalks; are hexapetalous, of a deep yellow Colour, with long *Apices* of the same Colour: They grow in shallow, fresh Water Ponds, in the Woods of *Virginia* and *Carolina,* and in the beginning of *February* adorn the Woods, when few other Plants appear in Blossom: The Flowers are succeeded by small round Capsula's, which in *March* and *April* divide into four Parts and disclose their Seeds, which are very small, and being dispersed by the Wind into watery Places, spring up very thick and blossom in a short Time.

As drawn, the flowers appear to resemble an *Hypericum,* and the habit perhaps *Hypericum densiflorum* Pursh. However, the alternate leaves, the flowering time, and the description of the fruit negate this suggestion. No supporting specimens were located.

2: *t. 52, plant. Frutex Lauri longiore folio.*

Ewan (1974, p. 97) suggested *Decumaria barbara* L. for this illustration (see FIGURE 2), recognizing aberrancies in the habit, the leaves, and the shape of the flower.

Catesby (**2:** 52) described the plant as follows:

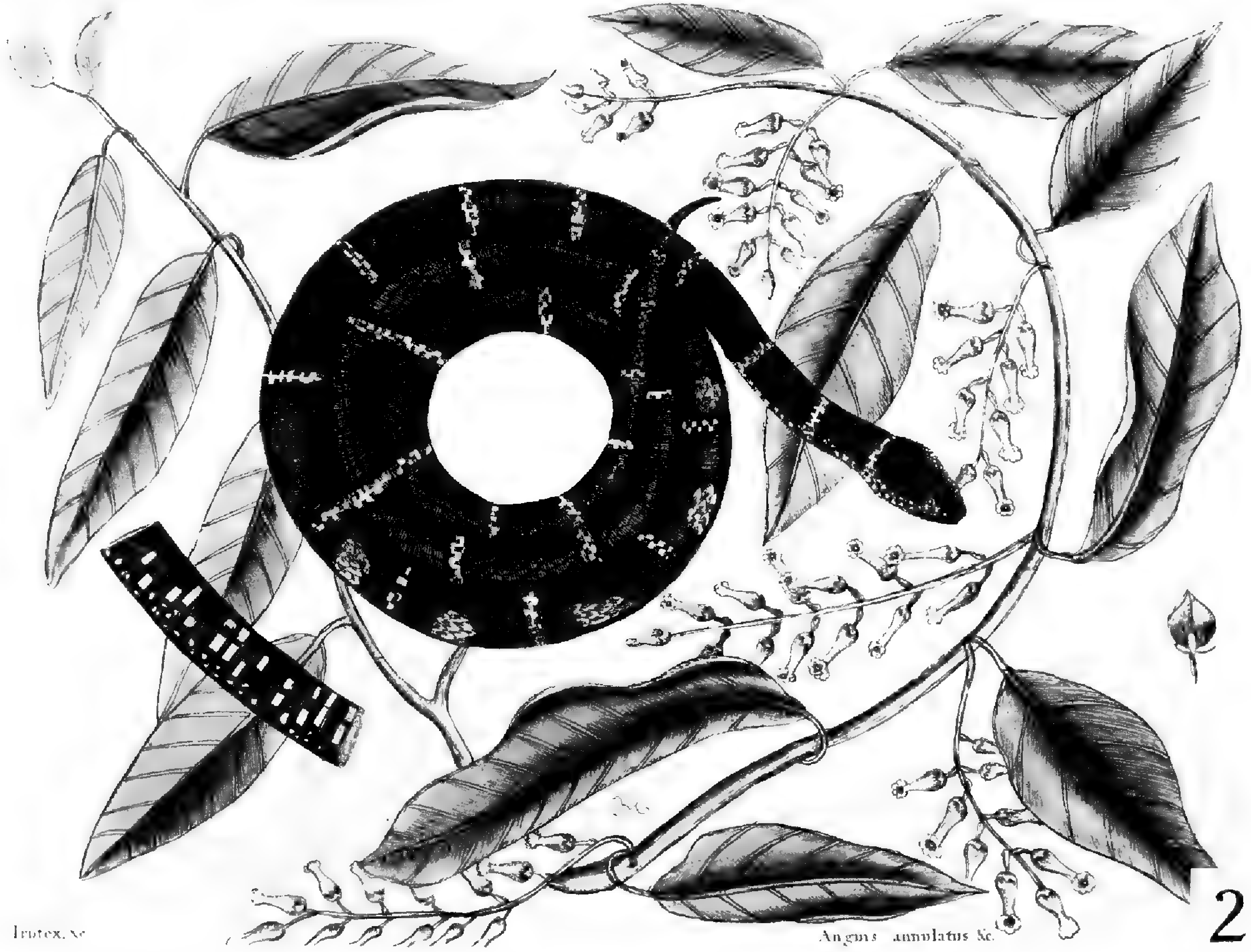

FIGURE 2. Catesby's illustration of "Frutex Lauri longiore folio" (Vol. 2, *t. 52*). Unidentified.

> This Shrub is a Native of *Virginia*, and grows in wet Swamps and standing Waters; it rises from the Ground, with many Stems to the Height of eight or ten Feet, of a reddish Colour. The Leaves are placed alternately an Inch from one another, and are in Shape like those of a Bay, stiff and shining; at the Pedicles of the Leaves grow the Flowers, which are tubulous, of a pale red Colour, and set on Stalks two and three Inches long; these Flowers are succeded by small conic Seed-Vessels about the Size of large Peas, which when ripe, open in two Parts and display many small black Seeds. It retains the Leaves all the Winter.

If the bilobed capsule, as drawn, is associated with what appears to be a tubular corolla, the plant may be in the Apocynaceae. We know of no plant that agrees with the characters given in the description. We doubt that it is *Decumaria*. Again, no supporting specimens were located.

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APPENDIX. **Determinations of Catesby's Illustrations of Plants**

VOLUME 1

9. **Castanea pumila** (L.) Miller—Fagaceae
10. **Colubrina elliptica** (Sw.) Briz. & Stern—Rhamnaceae
11. **Taxodium distichum** (L.) Rich.—Taxodiaceae
13. **Myrica pensylvanica** Loisel—Myricaceae
14. **Oryza sativa** L.—Gramineae
15. **Smilax laurifolia** L.—Smilacaceae
16. **Quercus phellos** L.—Fagaceae
17. **Quercus virginiana** Miller—Fagaceae
18. **Quercus prinus** L.—Fagaceae
19. **Quercus marilandica** Muenchh.*—Fagaceae
20, above. **Quercus nigra** L.—Fagaceae
20, below. **Mitchella repens** L.—Rubiaceae
21, left. **Quercus alba** L.—Fagaceae
21, right. **Quercus rubra** L.—Fagaceae
22. **Quercus incana** Bartram (*Quercus cinerea* Michx.*)—Fagaceae
23. **Quercus laevis** Walter (*Quercus catesbaei* Michx.*)—Fagaceae
24. **Podophyllum peltatum** L.—Berberidaceae
25. **Chrysobalanus icaco** L.—Chrysobalanaceae
26. **Zanthoxylum clava-herculis** L.—Rutaceae
27. **Cornus florida** L. forma **rubra** (Weston) Schelle—Cornaceae
28. **Prunus virginiana** L.—Rosaceae
29. **Aristolochia serpentaria** L.—Aristolochiaceae
30. **Bursera simaruba** (L.) Sarg.—Burseraceae
31. **Ilex cassine** L.—Aquifoliaceae
32. **Uniola paniculata** L.—Gramineae
33. **Hypoxis** sp.—Hypoxidaceae
34. **Populus heterophylla** L.—Salicaceae
35. **Ipomoea sagittata** Poiret—Convolvulaceae
36. **Monotropa uniflora** L.—Monotropaceae
37. **Tabebuia bahamensis** (Northrop) Britton—Bignoniaceae
38. **Carya alba** (L.) K. Koch—Juglandaceae; **Carya cordiformis** (Wangenh.) K. Koch—Juglandaceae (smaller fruit)
39. **Magnolia virginiana** L. (*Magnolia virginiana* var. *glauca* L.*)—Magnoliaceae
40. **Metopium toxiferum** (L.) Krug & Urban—Anacardiaceae
41. **Nyssa sylvatica** Marsh.—Nyssaceae
42. **Jacaranda caerulea** (L.) Griseb.* (*Bignonia caerulea* L.*)—Bignoniaceae
43. **Gleditsia aquatica** Marsh.—Leguminosae
44. **Gordonia lasianthus** (L.) Ellis—Theaceae
45. **Trillium catesbaei** Ell.*—Liliaceae
46. **Calycanthus floridus** L.—Calycanthaceae
47. **Smilax pumila** Walter—Smilacaceae
48. **Liriodendron tulipifera** L.—Magnoliaceae
49. **Catalpa bignonioides** Walter—Bignoniaceae
50. **Trillium maculatum** Raf.*—Liliaceae
51. **Cocculus carolinus** (L.) DC. (*Cissampelos smilacina* L.*)—Menispermaceae
52. **Smilax tamnoides** L.—Smilacaceae
53. **Gelsemium sempervirens** (L.) Aiton—Loganiaceae
54. **Symplocos tinctoria** (L.) L'Hér.—Symplocaceae
55. **Sassafras albidum** (Nutt.) Nees var. **molle** (Raf.) Fern.—Lauraceae

*Names determined to be based on Catesby's illustrations.

56. **Platanus occidentalis** L.—Platanaceae
57. **Rhododendron viscosum** (L.) Torrey var. **aemulans** Rehder—Ericaceae
58, above. **Cleistes divaricata** (L.) Ames—Orchidaceae
58, below. **Echites umbellata** Jacq.—Apocynaceae
59. **Casasia clusiifolia** (Jacq.) Urban—Rubiaceae
60. **Nyssa aquatica** L.*—Nyssaceae
61. **Osmanthus americanus** (L.) Gray—Oleaceae
62. **Acer rubrum** L.—Aceraceae
63. **Persea borbonia** (L.) Sprengel* (*Laurus borbonia* L.*)—Lauraceae
64. **Halesia tetraptera** Ellis—Styracaceae
65. **Campsis radicans** (L.) Seem.—Bignoniaceae
66. **Clethra alnifolia** L.—Clethraceae
67. **Juglans nigra** L.—Juglandaceae
68. **Chionanthus virginicus** L.—Oleaceae
69. **Myrica cerifera** L.—Myricaceae
70. **Gentiana catesbaei** Walter—Gentianaceae
71. **Oxydendrum arboreum** (L.) DC.*—Ericaceae
72. **Salmea petrobioides** Griseb.—Compositae
75. **Reynosia septentrionalis** Urban—Rhamnaceae
77. **Phymosia abutiloides** (L.) Ham.—Malvaceae
79. **Scaevola plumieri** (L.) Vahl* (*Lobelia plumierii* L.*)—Goodeniaceae
80. **Fraxinus americana** L.—Oleaceae
82. **Orontium aquaticum** L.—Araceae
83. **Peltandra virginica** (L.) Schott & Engler—Araceae
85. **Avicennia germinans** (L.) L.—Verbenaceae
86. **Laguncularia racemosa** (L.) Gaertner—Combretaceae
92. **Wedelia bahamensis** (Britton) Schulz—Compositae
93. **Borrichia arborescens** (L.) DC.—Compositae
98. **Jacquinia keyensis** Mez—Theophrastaceae

VOLUME 2

24. **Dalbergia ecastophyllum** (L.) Taub.—Leguminosae
26. **Phyllanthus epiphyllanthus** L.—Euphorbiaceae
28. above. **Ocotea coriacea** (Sw.) Britton (*Laurus catesbyana* Michx.*)—Lauraceae
28. below. **Galactia rudolphioides** (Griseb.) Bentham & Hooker—Leguminosae
30. Unidentified
32. **Picrodendron baccatum** (L.) Krug & Urban—Euphorbiaceae
33. above. **Conocarpus erectus** L.—Combretaceae
33. below. **Amyris elemifera** L.—Rutaceae
38. **Thalassia testudinum** König—Hydrocharitaceae
42. left. **Lysiloma latisiliquum** (L.) Bentham—Leguminosae
42. right. **Banara minutiflora** (A. Rich.) Sleumer—Flacourtiaceae
43. **Leucothoë racemosa** (L.) Gray—Ericaceae
44. **Acacia tortuosa** (L.) Willd.—Leguminosae
45. **Alocasia** sp. or **Xanthosoma** sp.—Araceae
46. **Croton eluteria** (L.) Sw.* (*Clutea eluteria* L.*, *Clutia cascarilla* L.*)—Euphorbiaceae
47. **Callicarpa americana** L.—Verbenaceae
48. **Cissus tuberculata** Jacq.—Vitaceae
49. **Erythrina herbacea** L.—Leguminosae
50. **Canella winterana** (L.) Gaertner—Canellaceae
51. above. **Caesalpinia bahamensis** Lam.—Leguminosae
51. below. **Passiflora suberosa** L.—Passifloraceae
52. Unidentified

53. **Urechites lutea** (L.) Britton* (*Vinca lutea* L.*, *Echites catesbaei* G. Don*)—Apocynaceae
54. **Silene virginica** L.—Caryophyllaceae
55. **Polystachya concreta** (Jacq.) Garay & Sweet—Orchidaceae
56. **Lilium superbum** L.—Liliaceae
57. **Ilex vomitoria** L. (*Cassine paragua* Miller*)—Aquifoliaceae
58. **Lilium catesbaei** Walter—Liliaceae
59. **Echinacea purpurea** (L.) Moench—Compositae
60. **Ipomoea batatas** (L.) Lam.—Convolvulaceae
61. **Magnolia grandiflora** L.—Magnoliaceae
62. **Commelina virginica** L.—Commelinaceae
63. **Rhizophora mangle** L.—Rhizophoraceae
64. **Annona glabra** L.*—Annonaceae
65. **Liquidambar styraciflua** L.—Hamamelidaceae
66. **Haematoxylon campechianum** L.—Leguminosae
67. **Annona glabra** L.—Annonaceae
68. **Epidendrum nocturnum** Jacq.—Orchidaceae
69. **Sarracenia × catesbaei** (Ell.) Bell*—Sarraceniaceae
70. **Sarracenia purpurea** L.—Sarraceniaceae
71. **Symplocarpus foetidus** (L.) Nutt.—Araceae
72. **Cypripedium acaule** Aiton (*Cypripedium vittatum* var. *planum* Raf.*)—Orchidaceae
73. **Cypripedium pubescens** Willd. (*Cypripedium vittatum* var. *tortile* Raf.*)—Orchidaceae
74. **Epidendrum boothianum** Lindley—Orchidaceae
75. **Mastichodendron foetidissimum** (Jacq.) Lam—Sapotaceae
76. **Diospyros virginiana** L.—Ebenaceae
77. **Catopsis berteroniana** (Schultes) Mez—Bromeliaceae
78. **Spigelia marilandica** (L.) L.—Loganiaceae
79. **Bourreria ovata** Miers—Boraginaceae
80. **Magnolia tripetala** (L.) L.* (*Magnolia virginiana* var. *tripetala* L.*)—Magnoliaceae
81. above. **Swietenia mahagoni** (L.) Jacq. (*Cedrela mahag.* L.*)—Meliaceae
81. below. **Phoradendron rubrum** (L.) Griseb.* (*Viscum rubrum* L.*)—Loranthaceae
82. **Bignonia capreolata** L.—Bignoniaceae
83. **Ptelea trifoliata** L.—Rutaceae
84. above. **Philadelphus inodorus** L.*—Saxifragaceae
84. below. **Smilax lanceolata** L.—Smilacaceae
85. **Asimina triloba** (L.) Dunal* (*Annona triloba* L.*)—Annonaceae
86. **Annona reticulata** L.—Annonaceae
87. above. **Manilkara bahamensis** Lam & Meeuse (*Sloanea emarginata* L.*)—Sapotaceae
87. below. **Ipomoea microdactyla** Griseb.—Convolvulaceae
88. left. **Epidendrum plicatum** Lindley—Orchidaceae
88. right. **Epidendrum cochleatum** L.—Orchidaceae
89. **Tillandsia balbisiana** (Schultes) Roemer & Schultes—Bromeliaceae
90. **Hibiscus tiliaceus** L.—Malvaceae
91. above. **Cordia sebestena** L.—Boraginaceae
91. below. **Ipomoea carolina** L.*—Convolvulaceae
92. **Plumeria rubra** L.—Apocynaceae
93. above. **Plumeria obtusa** L.*—Apocynaceae
93. below. **Passiflora cuprea** L.*—Passifloraceae
94. **Coccoloba diversifolia** Jacq.—Polygonaceae
95. above. **Hippomane mancinella** L.—Euphorbiaceae

95. below. **Dendropemon purpureum** (L.) Krug & Urban* (*Viscum purpureum* L.*)—Loranthaceae
96. **Coccoloba uvifera** (L.) L.—Polygonaceae
97. **Pithecellobium bahamense** Northrop—Leguminosae
98. **Kalmia latifolia** L.—Ericaceae
99. **Clusia rosea** Jacq.—Clusiaceae
100. **Catesbaea spinosa** L.* (*Catesbaea* L.*)—Rubiaceae

APPENDIX

1. **Dodecatheon meadia** L.*—Primulaceae
2. **Hamamelis virginiana** L.—Hamamelidaceae
3. **Cypripedium acaule** Aiton (*Cypripedium catesbianum* Raf.*)—Orchidaceae
4. **Rhus glabra** L.—Anacardiaceae
5. **Hymenocallis caroliniana** (L.) Herb.* (*Pancratium carolinianum* L.*)—Amaryllidaceae
6. **Theobroma cacao** L.*—Sterculiaceae
7. **Vanilla mexicana** Miller—Orchidaceae
8. **Lilium philadelphicum** L.—Liliaceae
9. **Anacardium occidentale** L.—Anacardiaceae
11. **Lilium canadense** L.—Liliaceae
12. **Zephyranthes atamasco** (L.) Herb.—Amaryllidaceae
13. **Stewartia malacodendron** L.—Theaceae
15. **Magnolia acuminata** (L.) L.* (*Magnolia virginiana* var. *acuminata* L.*)—Magnoliaceae
16. **Panax quinquefolius** L.—Araliaceae
17. left. **Kalmia angustifolia** L.—Ericaceae
17. right. **Rhododendron maximum** L.—Ericaceae
18. **Ficus citrifolia** Miller—Moraceae
20. **Robinia hispida** L.—Leguminosae

ARNOLD ARBORETUM
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

INDEXES TO PAPERS 1 TO 100 PUBLISHED AS PARTS OF THE GENERIC FLORA OF THE SOUTHEASTERN UNITED STATES

CARROLL E. WOOD, JR.

WITH THE PUBLICATION of the one-hundredth paper in the continuing series dealing with the genera and families of seed-bearing plants in the southeastern United States, it seems appropriate, especially in response to numerous inquiries, to provide indexes to the papers themselves, their authors, the families and genera treated, and the published illustrations of genera. This information is given here in four parts:

I. Chronological List of Papers Published in the Generic Flora
II. Authors and Titles of Papers Published in the Generic Flora
III. Index to Family Treatments Published in the Generic Flora
IV. Index to Generic Treatments and Illustrations Published in the Generic Flora

All of the indexed papers have appeared in the *Journal of the Arnold Arboretum,* beginning in July, 1958 (Volume 48, Number 3), and continuing to the present. Thirty-three authors have contributed to the series. All of the papers have been edited by C. E. Wood, Jr., and the last thirteen have been edited by Norton G. Miller, as well. Bernice G. Schubert, Elizabeth B. Schmidt, and Stephen A. Spongberg have contributed greatly in their roles as editors of the *Journal.* Barbara Nimblett and George K. Rogers have helped in various ways with the present indexes.

The hundred papers include 130 families, of which the Compositae and Leguminosae have not yet been treated in full. As published in these papers, 475 genera have been recognized; subsequent taxonomic realignments have suggested that a few additional segregate genera should be recognized, however, and these have been indexed as such. In a few instances conservation or a more inclusive generic concept has changed a generic name (e.g., *Chamaedaphne* conserved over *Cassandra*; *Myrsine,* including *Rapanea*).

The principal synonyms of families and genera are included in the respective indexes. In addition, all familial and generic names recognized by John K. Small in his *Manual of the Southeastern Flora* (New York, 1930; republished by University of North Carolina Press, Chapel Hill, 1961) have been included, along with their equivalents, since the concepts of family and genus used in the Generic Flora generally are broader than those of Small.

From the beginning of the series, publication of completed familial and generic treatments has not been delayed pending completion of suitable illustrations, although the ultimate goal has been to have at least one illustration

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for each family. One hundred ninety-five genera are illustrated in the published papers. Subsequently, illustrations of 98 others treated in these papers have been prepared, and it is hoped that all of these can be made available eventually. Twenty-one of the 98 are included (with captions directly on the illustrations) in C. E. Wood, Jr., *A Student's Atlas of Flowering Plants: Some Dicotyledons of Eastern North America,* or in A. E. Radford *et al., Vascular Plant Systematics* (both published by Harper & Row, New York, 1974).

I. CHRONOLOGICAL LIST OF PAPERS IN THE GENERIC FLORA OF THE SOUTHEASTERN UNITED STATES

The papers are numbered in the sequence of their publication, although the position of each in the series was not designated in most of the earlier ones. The family (or families) treated in each paper is listed, along with the surname of the author(s) and the volume, inclusive pages, and year of publication in the *Journal of the Arnold Arboretum.* Full titles of papers and initials of authors are given in the index of authors and papers.

PAPER NUMBER AND FAMILY OR FAMILIES TREATED	AUTHOR(S)	JOUR. ARNOLD ARB. VOLUME-PAGES-YEAR		
1. Magnoliaceae, Annonaceae, Illiciaceae, Schisandraceae, Canellaceae, Calycanthaceae, Lauraceae	Wood	**39:**	296–346.	1958
2. Nymphaeaceae, Ceratophyllaceae	Wood	**40:**	94–112.	1959
3. Empetraceae, Diapensiaceae	Wood & Channell		161–171.	
4. Theophrastaceae, Myrsinaceae, Primulaceae	Wood & Channell		268–288.	
5. Oleaceae	Wilson & Wood		369–384.	
6. Plumbaginaceae	Channell & Wood		391–397.	
7. Theaceae	Wood		413–419.	
8. Sapotaceae, Ebenaceae, Styracaceae, Symplocaceae	Wood & Channell	**41:**	1–35.	1960
9. Araceae, Lemnaceae	Wilson		47–72.	
10. Sarraceniaceae, Droseraceae	Wood		152–163.	
11. Hydrophyllaceae, Polemoniaceae	Wilson		197–212.	
12. Myrtaceae	Wilson		270–278.	
13. Convolvulaceae	Wilson		298–317.	
14. Ericaceae	Wood	**42:**	10–80.	1961
15. Cyrillaceae, Clethraceae	Thomas		96–106.	
16. Turneraceae, Passifloraceae	Brizicky		204–218.	
17. Violaceae	Brizicky		321–333.	
18. Rutaceae	Brizicky	**43:**	1–22.	1962
19. Simaroubaceae, Burseraceae	Brizicky		173–186.	
20. Papaveraceae, Fumariaceae	Ernst		315–343.	
21. Anacardiaceae	Brizicky		359–375.	
22. Thymelaeaceae	Nevling		428–434.	
23. Leitneriaceae	Channell & Wood		435–438.	
24. Capparaceae, Moringaceae	Ernst	**44:**	81–95.	1963
25. Loasaceae	Ernst & Thompson		138–142.	

Paper Number and Family or Families Treated	Author(s)	Jour. Arnold Arb. Volume-Pages-Year		
26. Hamamelidaceae, Platanaceae	Ernst	**44:**	193–210.	1963
27. Tribes of Compositae	Solbrig		436–461.	
28. Sapindaceae, Aceraceae, Hippocastanaceae	Brizicky		462–501.	
29. Berberidaceae, Lardizabalaceae, Menispermaceae	Ernst	**45:**	1–35.	1964
30. Celastraceae, Hippocrateaceae, Aquifoliaceae	Brizicky		206–234.	
31. Lythraceae	Graham		235–250.	
32. Elaeagnaceae	Graham		274–278.	
33. Rhizophoraceae, Combretaceae	Graham		285–301.	
34. Cistaceae	Brizicky		346–357.	
35. Rhamnaceae	Brizicky		439–463.	
36. Vitaceae	Brizicky	**46:**	48–67.	1965
37. Polygonaceae	Graham & Wood		91–121.	
38. Valerianaceae, Dipsacaceae	Ferguson		218–231.	
39. Tiliaceae, Elaeocarpaceae	Brizicky		286–307.	
40. Caprifoliaceae	Ferguson	**47:**	33–59.	1966
41. Sterculiaceae	Brizicky		60–74.	
42. Cornaceae	Ferguson		106–116.	
43. Nyssaceae	Eyde		117–125.	
44. Araliaceae	Graham		126–136.	
45. Goodeniaceae	Brizicky		293–300.	
46. Euphorbiaceae	Webster	**48:**	303–430.	1967
47. Compositae-Senecioneae	Vuilleumier	**50:**	104–123.	1969
48. Portulacaceae, Basellaceae	Bogle		566–598.	
49. Compositae-Mutisieae	Vuilleumier		620–625.	
50. Ulmaceae	Elias	**51:**	18–40.	1970
51. Cannabaceae	Miller		185–203.	
52. Acanthaceae	Long		257–309.	
53. Molluginaceae, Aizoaceae	Bogle		431–462.	
54. Chrysobalanaceae	Prance		521–528.	
55. Urticaceae	Miller	**52:**	40–68.	1971
56. Fagaceae	Elias		159–195.	
57. Staphyleaceae	Spongberg		196–203.	
58. Polygalaceae	Miller		267–284.	
59. Myricaceae	Elias		305–318.	
60. Orobanchaceae	Thieret		404–434.	
61. Saururaceae	Wood		479–485.	
62. Linaceae	Robertson		649–665.	
63. Juglandaceae	Elias	**53:**	26–51.	1972
64. Malpighiaceae	Robertson		101–112.	
65. Geraniaceae	Robertson		182–201.	
66. Phrymaceae	Thieret		226–233.	
67. Saxifragaceae	Spongberg		409–498.	
68. Zygophyllaceae	Porter		531–552.	
69. Compositae-Lactuceae	Vuilleumier	**54:**	42–93.	1973
70. Krameriaceae	Robertson		322–327.	
71. Nyctaginaceae	Bogle	**55:**	1–37.	1974
72. Leguminosae-Mimosoideae	Elias		67–118.	
73. Rosaceae	Robertson		303–332. 344–401. 611–662.	

PAPER NUMBER AND FAMILY OR FAMILIES TREATED	AUTHOR(S)	JOUR. ARNOLD ARB. VOLUME-PAGES-YEAR	
74. Oxalidaceae	Robertson	**56:** 223–239.	1975
75. Mayacaceae	Thieret	248–255.	
76. Bromeliaceae	Smith & Wood	375–397.	
77. Balsaminaceae	Wood	413–426.	
78. Podostemaceae	Graham & Wood	456–465.	
79. Leguminosae-Caesalpinioideae	Robertson & Lee	**57:** 1–53.	1976
80. Guttiferae (Clusiaceae)	Adams & Wood	74–90.	
81. Haemodoraceae	Robertson	205–216.	
82. Martyniaceae	Thieret	**58:** 25–39.	1977
83. Najadaceae	Haynes	161–170.	
84. Potamogetonaceae	Haynes	**59:** 170–191.	1978
85. Crassulaceae	Spongberg	197–248.	
86. Amaranthaceae	Robertson	**62:** 267–314.	1981
87. Stemonaceae	Rogers	**63:** 327–336.	1982
88. Sparganiaceae	Thieret	341–356.	
89. Casuarinaceae	Rogers	357–373.	
90. Bataceae	Rogers	375–386.	
91. Olacaceae	Robertson	387–399.	
92. Viscaceae	Kuijt	401–410.	
93. Caricaceae	Miller	411–427.	
94. Melastomataceae	Wurdack & Kral	429–439.	
95. Gentianaceae	Wood & Weaver	441–487.	
96. Compositae-Vernonieae	Jones	489–507.	
97. Burmanniaceae	Wood	**64:** 293–307.	1983
98. Alismataceae	Rogers	387–424.	
99. Xyridaceae	Kral	425–433.	
100. Menyanthaceae	Wood	435–449.	

II. AUTHORS AND TITLES OF PAPERS PUBLISHED IN THE GENERIC FLORA OF THE SOUTHEASTERN UNITED STATES

Under each author or pair of authors, papers are arranged chronologically. Volume numbers, pages, and dates refer to the *Journal of the Arnold Arboretum.*

ADAMS, P., & C. E. WOOD, JR.

The genera of Guttiferae (Clusiaceae) in the southeastern United States. **57:** 74–90. 1976.

BOGLE, A. L.

The genera of Portulacaceae and Basellaceae in the southeastern United States. **50:** 566–598. 1969.

The genera of Molluginaceae and Aizoaceae in the southeastern United States. **51:** 431–462. 1970.

The genera of Nyctaginaceae in the southeastern United States. **55:** 1–37. 1974.

BRIZICKY, G. K.

The genera of Turneraceae and Passifloraceae in the southeastern United States. **42:** 204–218. 1961.

The genera of Violaceae in the southeastern United States. **42:** 321–333. 1961.

The genera of Rutaceae in the southeastern United States. **43:** 1–22. 1962.

The genera of Simaroubaceae and Burseraceae in the southeastern United States. **43:** 173–186. 1962.
The genera of Anacardiaceae in the southeastern United States. **43:** 359–375. 1962.
The genera of Sapindales in the southeastern United States. **44:** 462–501. 1963.
The genera of Celastrales in the southeastern United States. **45:** 206–234. 1964.
The genera of Cistaceae in the southeastern United States. **45:** 346–357. 1964.
The genera of Rhamnaceae in the southeastern United States. **45:** 439–463. 1964.
The genera of Vitaceae in the southeastern United States. **46:** 48–67. 1965.
The genera of Tiliaceae and Elaeocarpaceae in the southeastern United States. **46:** 286–307. 1965.
The genera of Sterculiaceae in the southeastern United States. **47:** 60–74. 1966.
The Goodeniaceae in the southeastern United States. **47:** 293–300. 1966.

CHANNELL, R. B., & C. E. WOOD, JR. (see also WOOD & CHANNELL)
The genera of the Primulales of the southeastern United States. **40:** 268–288. 1959.
The genera of Plumbaginaceae of the southeastern United States. **40:** 391–397. 1959.
The Leitneriaceae in the southeastern United States. **43:** 435–438. 1962.

ELIAS, T. S.
The genera of Ulmaceae in the southeastern United States. **51:** 18–40. 1970.
The genera of Fagaceae in the southeastern United States. **52:** 159–195. 1971.
The genera of Myricaceae in the southeastern United States. **52:** 305–318. 1971.
The genera of Juglandaceae in the southeastern United States. **53:** 26–51. 1972.
The genera of Mimosoideae (Leguminosae) in the southeastern United States. **55:** 67–118. 1974.

ERNST, W. R.
The genera of Papaveraceae and Fumariaceae in the southeastern United States. **43:** 315–343. 1962.
The genera of Capparaceae and Moringaceae in the southeastern United States. **44:** 81–95. 1963.
The genera of Hamamelidaceae and Platanaceae in the southeastern United States. **44:** 193–210. 1963.
The genera of Berberidaceae, Lardizabalaceae, and Menispermaceae in the southeastern United States. **45:** 1–35. 1964.

——— & H. J. THOMPSON
The Loasaceae in the southeastern United States. **44:** 138–142. 1963.

EYDE, R. H.
The Nyssaceae in the southeastern United States. **47:** 117–125. 1966.

FERGUSON, I. K.
The genera of Valerianaceae and Dipsacaceae in the southeastern United States. **46:** 218–231. 1965.
The genera of Caprifoliaceae in the southeastern United States. **47:** 33–59. 1966.
The Cornaceae in the southeastern United States. **47:** 106–116. 1966.

GRAHAM, S. A.
The genera of Lythraceae in the southeastern United States. **45:** 235–250. 1964.
The Elaeagnaceae in the southeastern United States. **45:** 274–278. 1964.
The genera of Rhizophoraceae and Combretaceae in the southeastern United States. **45:** 285–301. 1964.
The genera of Araliaceae in the southeastern United States. **47:** 126–136. 1966.

——— & C. E. WOOD, JR.
The genera of Polygonaceae in the southeastern United States. **46:** 91–121. 1965.
The Podostemaceae in the southeastern United States. **56:** 456–465. 1975.

HAYNES, R. R.
The Najadaceae in the southeastern United States. **58:** 161–170. 1977.
The Potamogetonaceae in the southeastern United States. **59:** 170–191. 1978.

JONES, S. B., JR.
The genera of the Vernonieae (Compositae) in the southeastern United States. **63:** 489–507. 1982.
KRAL, R. (see also WURDACK & KRAL)
The Xyridaceae in the southeastern United States. **64:** 425–433. 1983.
KUIJT, J.
The Viscaceae in the southeastern United States. **63:** 401–410. 1982.
LEE, Y. T. (see ROBERTSON & LEE)
LONG, R. W.
The genera of Acanthaceae in the southeastern United States. **51:** 257–309. 1970.
MILLER, N. G.
The genera of the Cannabaceae in the southeastern United States. **51:** 185–203. 1970.
The genera of the Urticaceae in the southeastern United States. **52:** 40–68. 1971.
The Polygalaceae in the southeastern United States. **52:** 267–284. 1971.
The Caricaceae in the southeastern United States. **63:** 411–427. 1982.
NEVLING, L. I., JR.
The Thymelaeaceae in the southeastern United States. **43:** 428–434. 1962.
PORTER, D. M.
The genera of Zygophyllaceae in the southeastern United States. **53:** 531–552. 1972.
PRANCE, G. T.
The genera of Chrysobalanaceae in the southeastern United States. **51:** 521–528. 1970.
ROBERTSON, K. R.
The Linaceae in the southeastern United States. **52:** 649–665. 1971.
The Malpighiaceae in the southeastern United States. **53:** 101–112. 1972.
The genera of Geraniaceae in the southeastern United States. **53:** 182–201. 1972.
The Krameriaceae in the southeastern United States. **54:** 322–327. 1973.
The genera of Rosaceae in the southeastern United States. **55:** 303–332, 344–401, 611–662. 1974.
The Oxalidaceae in the southeastern United States. **56:** 223–239. 1975.
The genera of Haemodoraceae in the southeastern United States. **57:** 205–216. 1976.
The genera of Amaranthaceae in the southeastern United States. **62:** 267–314. 1981.
The genera of Olacaceae in the southeastern United States. **63:** 387–399. 1982.
——— & Y. T. LEE
The genera of Caesalpinioideae (Leguminosae) in the southeastern United States. **57:** 1–53. 1976.
ROGERS, G. K.
The Stemonaceae in the southeastern United States. **63:** 327–336. 1982.
The Casuarinaceae in the southeastern United States. **63:** 357–373. 1982.
The Bataceae in the southeastern United States. **63:** 375–386. 1982.
The genera of Alismataceae in the southeastern United States. **64:** 387–424. 1983.
SMITH, L. B., & C. E. WOOD, JR.
The genera of Bromeliaceae in the southeastern United States. **56:** 375–397. 1975.
SOLBRIG, O. T.
The tribes of Compositae in the southeastern United States. **44:** 436–461. 1963.
SPONGBERG, S. A.
The Staphyleaceae in the southeastern United States. **52:** 196–203. 1971.
The genera of Saxifragaceae in the southeastern United States. **53:** 409–498. 1972.
The genera of Crassulaceae in the southeastern United States. **59:** 197–248. 1978.
THIERET, J. W.
The genera of Orobanchaceae in the southeastern United States. **52:** 404–434. 1971.
The Phrymaceae in the southeastern United States. **53:** 226–233. 1972.
The Mayacaceae in the southeastern United States. **56:** 248–255. 1975.
The Martyniaceae in the southeastern United States. **58:** 25–39. 1977.
The Sparganiaceae in the southeastern United States. **63:** 341–356. 1982.

THOMAS, J. L.
The genera of the Cyrillaceae and Clethraceae of the southeastern United States. **42:** 96–106. 1961.
THOMPSON, H. J. (see ERNST & THOMPSON)
VUILLEUMIER, B. S.
The genera of Senecioneae in the southeastern United States. **50:** 104–123. 1969.
The tribe Mutisieae (Compositae) in the southeastern United States. **50:** 620–625. 1969.
The genera of Lactuceae (Compositae) in the southeastern United States. **54:** 42–93. 1973.
WEAVER, R. E., JR. (see WOOD & WEAVER)
WEBSTER, G. L.
The genera of Euphorbiaceae in the southeastern United States. **48:** 303–430. 1967.
WILSON, K. A.
The genera of the Arales in the southeastern United States. **41:** 47–72. 1960.
The genera of Hydrophyllaceae and Polemoniaceae in the southeastern United States. **41:** 197–212. 1960.
The genera of Myrtaceae in the southeastern United States. **41:** 270–278. 1960.
The genera of Convolvulaceae in the southeastern United States. **41:** 298–317. 1960.
——— & C. E. WOOD, JR.
The genera of Oleaceae in the southeastern United States. **40:** 369–384. 1959.
WOOD, C. E., JR. (see also ADAMS & WOOD, CHANNELL & WOOD, GRAHAM & WOOD, SMITH & WOOD, and WILSON & WOOD)
The genera of the woody Ranales in the southeastern United States. **39:** 296–346. 1958.
The genera of the Nymphaeaceae and Ceratophyllaceae in the southeastern United States. **40:** 94–112. 1959.
The genera of Theaceae of the southeastern United States. **40:** 413–419. 1959.
The genera of Sarraceniaceae and Droseraceae in the southeastern United States. **41:** 152–163. 1960.
The genera of Ericaceae in the southeastern United States. **42:** 10–80. 1961.
The Saururaceae in the southeastern United States. **52:** 479–485. 1971.
The Balsaminaceae in the southeastern United States. **56:** 413–426. 1975.
The genera of Burmanniaceae in the southeastern United States. **64:** 293–307. 1983.
The genera of Menyanthaceae in the southeastern United States. **64:** 435–449. 1983.
——— & R. B. CHANNELL
The Empetraceae and Diapensiaceae of the southeastern United States. **40:** 161–171. 1959.
The genera of the Ebenales in the southeastern United States. **41:** 1–35. 1960.
——— & R. E. WEAVER, JR.
The genera of Gentianaceae in the southeastern United States. **63:** 441–487. 1982.
WURDACK, J. J., & R. KRAL
The genera of Melastomataceae in the southeastern United States. **63:** 429–439. 1982.

III. INDEX TO FAMILIES PUBLISHED IN THE GENERIC FLORA SERIES

Volume, number of the first page of the article, and year of publication are given for each family or part of a family listed. All refer to the *Journal of the Arnold Arboretum.*

Acanthaceae	**51:** 257. 1970
Aceraceae	**44:** 481. 1963
Aesculaceae = Hippocastanaceae	
Aizoaceae	**51:** 443. 1970
Alismataceae	**64:** 387. 1983
Allionaceae = Nyctaginaceae	
Altingiaceae = Hamamelidaceae	
Amaranthaceae	**63:** 267. 1981
Amygdalaceae = Rosaceae	
Anacardiaceae	**43:** 359. 1962
Annonaceae	**39:** 309. 1958
Aquifoliaceae	**45:** 227. 1964
Araceae	**41:** 47. 1960
Araliaceae	**47:** 126. 1966
Ardisiaceae = Myrsinaceae	
Armeriaceae = Plumbaginaceae	
Asteraceae: see Compositae	
Balsaminaceae	**56:** 413. 1975
Basellaceae	**50:** 590. 1969
Bataceae	**63:** 375. 1982
Berberidaceae	**45:** 1. 1964
Bromeliaceae	**56:** 375. 1975
Brunoniaceae *sensu* Small = Goodeniaceae	
Burmanniaceae	**64:** 293. 1983
Burseraceae	**43:** 183. 1962
Byttneriaceae = Sterculiaceae	
Cabombaceae = Nymphaeaceae	
Caesalpiniaceae = Leguminosae	
Caesalpinioideae (Leguminosae)	**57:** 1. 1976
Calycanthaceae	**39:** 322. 1958
Canellaceae	**39:** 320. 1958
Cannabaceae	**51:** 185. 1970
Capparaceae	**44:** 81. 1963
Caprifoliaceae	**47:** 33. 1966
Caricaceae	**63:** 411. 1982
Cassiaceae = Leguminosae	
Cassythaceae = Lauraceae	
Casuarinaceae	**63:** 357. 1982
Celastraceae	**45:** 206. 1964
Ceratophyllaceae	**40:** 109. 1959
Chrysobalanaceae	**51:** 521. 1970
Cichoriaceae = Compositae-Lactuceae	
Cistaceae	**45:** 346. 1964
Clethraceae	**42:** 102. 1961
Clusiaceae: see Guttiferae	
Combretaceae	**45:** 293. 1964
Compositae	
Tribes of	**44:** 436. 1963
Anthemideae	**44:** 444. 1963
Arctoteae	**44:** 445. 1963
Astereae	**44:** 446. 1963
Calenduleae	**44:** 448. 1963

Cardueae	**44:** 448. 1963
Cichorieae = Lactuceae	
Eupatorieae	**44:** 452. 1963
Heliantheae	**44:** 453. 1963
Inuleae	**44:** 456. 1963
Lactuceae	**44:** 450. 1963 **54:** 42. 1973
Mutisieae	**44:** 457. 1963 **50:** 620. 1969
Senecioneae	**44:** 459. 1963 **50:** 104. 1969
Vernonieae	**44:** 460. 1963 **63:** 489. 1982
Convolvulaceae	**41:** 298. 1960
Cornaceae	**47:** 106. 1966
Crassulaceae	**59:** 197. 1978
Cuscutaceae = Convolvulaceae	
Cyrillaceae	**42:** 96. 1961
Daphnaceae = Thymelaeaceae	
Diapensiaceae	**40:** 164. 1959
Dichondraceae = Convolvulaceae	
Dionaeaceae = Droseraceae	
Dipsacaceae	**46:** 226. 1965
Dodonaeaceae = Sapindaceae	
Droseraceae	**41:** 156. 1960
Ebenaceae	**41:** 17. 1960
Elaeagnaceae	**45:** 274. 1964
Elaeocarpaceae	**46:** 304. 1965
Empetraceae	**40:** 162. 1959
Epilobiaceae = Onagraceae	
Ericaceae	**42:** 10. 1961
Euphorbiaceae	**48:** 303. 1967
Fabaceae: see Leguminosae	
Fagaceae	**52:** 159. 1971
Frangulaceae = Rhamnaceae	
Fumariaceae	**43:** 333. 1962
Galacaceae = Diapensiaceae	
Gentianaceae	**63:** 441. 1982
Geraniaceae	**53:** 182. 1972
Goodeniaceae	**47:** 293. 1966
Grossulariaceae = Saxifragaceae	
Guttiferae	**57:** 74. 1976
Haemodoraceae	**57:** 205. 1976
Hamamelidaceae	**44:** 193. 1963
Hederaceae = Araliaceae	
Hippocastanaceae	**44:** 495. 1963
Hippocrateaceae	**45:** 223. 1964
Hydrangeaceae = Saxifragaceae	
Hydroleaceae = Hydrophyllaceae	
Hydrophyllaceae	**41:** 197. 1960
Hypericaceae = Guttiferae	
Illiciaceae	**39:** 315. 1958
Iteaceae = Saxifragaceae	
Juglandaceae	**53:** 26. 1972

Krameriaceae	**54**: 322. 1973
Lactuceae (Compositae)	**54**: 42. 1973
Lardizabalaceae	**45**: 20. 1964
Lauraceae	**39**: 326. 1958
Leguminosae	
Caesalpinioideae	**57**: 1. 1976
Mimosoideae	**55**: 67. 1974
Leitneriaceae	**43**: 435. 1962
Lemnaceae	**41**: 63. 1960
Linaceae	**52**: 649. 1971
Loasaceae	**44**: 138. 1963
Loranthaceae: see Viscaceae	
Lythraceae	**45**: 235. 1964
Magnoliaceae	**39**: 299. 1958
Malaceae = Rosaceae	
Malpighiaceae	**53**: 101. 1972
Martyniaceae	**58**: 25. 1977
Mayacaceae	**56**: 248. 1975
Melastomataceae	**63**: 429. 1982
Menispermaceae	**45**: 23. 1964
Menyanthaceae	**64**: 435. 1983
Mimosaceae = Leguminosae	
Mimosoideae (Leguminosae)	**55**: 67. 1974
Molluginaceae	**51**: 431. 1970
Monotropaceae = Ericaceae	
Morinaceae = Dipsacaceae	
Moringaceae	**44**: 93. 1963
Mutisieae (Compositae)	**50**: 620. 1969
Myricaceae	**52**: 305. 1971
Myrsinaceae	**40**: 271. 1959
Myrtaceae	**41**: 270. 1960
Najadaceae	**58**: 161. 1977
Nelumbonaceae = Nymphaeaceae	
Nyctaginaceae	**55**: 1. 1974
Nymphaeaceae	**40**: 94. 1959
Nyssaceae	**47**: 117. 1966
Olacaceae	**63**: 387. 1982
Oleaceae	**40**: 370. 1959
Orobanchaceae	**52**: 404. 1971
Oxalidaceae	**56**: 223. 1975
Papaveraceae	**43**: 315. 1962
Papayaceae = Caricaceae	
Parnassiaceae = Saxifragaceae	
Passifloraceae	**42**: 209. 1961
Penthoraceae = Saxifragaceae	
Phrymaceae	**53**: 226. 1972
Pisoniaceae = Nyctaginaceae	
Platanaceae	**44**: 206. 1963
Plumbaginaceae	**40**: 391. 1959
Podophyllaceae = Berberidaceae	
Podostemaceae	**56**: 456. 1975
Polemoniaceae	**41**: 205. 1960
Polygalaceae	**52**: 267. 1971
Polygonaceae	**46**: 91. 1965
Portulacaceae	**50**: 566. 1969
Potamogetonaceae	**59**: 170. 1978
Primulaceae	**40**: 273. 1959
Pyrolaceae = Ericaceae	
Rhamnaceae	**45**: 439. 1964
Rhizophoraceae	**45**: 285. 1964
Rosaceae	**55**: 303, 344, 611. 1974
Roxburghiaceae = Stemonaceae	
Ruppiaceae = Potamogetonaceae	
Rutaceae	**43**: 1. 1962
Sambucaceae = Caprifoliaceae	
Sapindaceae	**44**: 463. 1963
Sapotaceae	**41**: 2. 1960
Sarraceniaceae	**41**: 152. 1960
Saururaceae	**52**: 479. 1971
Saxifragaceae	**53**: 409. 1972
Schisandraceae	**39**: 318. 1958
Sedaceae = Crassulaceae	
Senecioneae (Compositae)	**50**: 104. 1969
Simaroubaceae	**43**: 173. 1962
Sparganiaceae	**63**: 341. 1982
Spondiaceae = Anacardiaceae	
Staphyleaceae	**53**: 196. 1971
Stemonaceae	**63**: 327. 1982
Sterculiaceae	**47**: 60. 1966
Styracaceae	**41**: 22. 1960
Surianaceae = Simaroubaceae	
Symplocaceae	**41**: 31. 1960
Terminaliaceae = Combretaceae	
Tetragoniaceae = Aizoaceae	
Theaceae	**40**: 413. 1959
Theophrastaceae	**40**: 269. 1959
Thymelaeaceae	**43**: 428. 1962
Tiliaceae	**46**: 286. 1965
Turneraceae	**42**: 204. 1961
Ulmaceae	**51**: 18. 1970
Urticaceae	**52**: 40. 1971
Vacciniaceae = Ericaceae	
Valerianaceae	**46**: 218. 1965
Vernonieae (Compositae)	**63**: 489. 1982
Violaceae	**42**: 321. 1961
Viscaceae	**63**: 401. 1982
Vitaceae	**46**: 48. 1965
Xyridaceae	**64**: 425. 1983
Zygophyllaceae	**53**: 531. 1972

IV. INDEX TO GENERIC TREATMENTS AND ILLUSTRATIONS PUBLISHED IN THE GENERIC FLORA SERIES

As in the preceding list of families, the references to genera include the volume number, the first page of each treatment, and the year in which each was published in the *Journal of the Arnold Arboretum*. Illustrated genera are marked with an asterisk. Pertinent synonyms are in italics, with a reference to the genus under which that name is treated. References in brackets pertain to genera included in a key but not admitted to the flora.

Benzoin = Lindera	
Berberis	**45:** 9. 1964
Berchemia	**45:** 457. 1964
Bicuculla = Dicentra	
Bilderdykia = Polygonum	
Biltia = Rhododendron	
Bivonea = Cnidoscolus	
Blechum	**51:** 284. 1970
Blutaparon	**62:** 312. 1981
*Boehmeria	**52:** 59. 1971
*Boerhavia	**55:** 23. 1974
Bolboxalis = Oxalis	
Bonamia	**41:** 306. 1960
Bothrocaryum = Cornus	
Boussingaultia: see Anredera	
Boykinia	**53:** 440. 1972
Brachyramphus = Launaea	
Brasenia	**40:** 103. 1959
Brayulinea = Guilleminea	
Breweria: see Bonamia	
Bruneria = Wolffia	
*Brunnichia	**46:** 119. 1965
Bryophyllum = Kalanchoë	
Bucida	**45:** 297. 1964
*Bumelia	**41:** 7. 1960
Burmannia	**64:** 300. 1983
Bursera	**43:** 185. 1962
Buxella = Gaylussacia	
*Byrsonima	**53:** 109. 1972
Cabomba	**40:** 102. 1959
Cacalia	**50:** 115. 1969
*Caesalpinia	**57:** 13. 1976
Cailleia = Dichrostachys	
Calonyction = Ipomoea	
Calophanes = Dyschoriste	
*Calycanthus	**39:** 323. 1958
*Calycocarpum	**45:** 28. 1964
Calyptranthes	**41:** 273. 1960
Calystegia	**41:** 308. 1960
Camphora = Cinnamomum	
Canella	**39:** 321. 1958
Cannabis	**51:** 188. 1970
Caperonia	**48:** 363. 1967
Capnoides = Corydalis	
Capparis	**44:** 85. 1963
Caraxeron: see Blutaparon	
Cardiospermum	**44:** 468. 1963
*Carica	**63:** 415. 1982
*Carya	**53:** 32. 1972
Cassandra = Chamaedaphne	
*Cassia	**57:** 35. 1976
Cassytha	**39:** 344. 1958
Castalia = Nymphaea	
*Castanea	**52:** 173. 1971
*Casuarina	**63:** 357. 1982
Cathartolinum = Linum	
*Catopsis	**56:** 392. 1975
Caulophyllum	**45:** 18. 1964
[Cayratia	**46:** 49. 1965]
Ceanothus	**45:** 451. 1964
Celastrus	**45:** 215. 1964
Celosia	**62:** 280. 1981
Celtis	**51:** 32. 1970
Centaurium	**63:** 453. 1982
Centrostachys = Achyranthes	
Centunculus = Anagallis	
Cerasus = Prunus	
*Ceratiola	**40:** 163. 1959
Ceratophyllum	**40:** 109. 1959
*Cercis	**57:** 48. 1976
Cerothamnus = Myrica	
Chaetoptelea = Ulmus	
Chamaechrista = Cassia	
*Chamaedaphne	**42:** 54. 1961
Chamaepericlymenum = Cornus	
*Chamaesyce	**48:** 420. 1967
*Chaptalia	**50:** 620. 1969
*Chelidonium	**43:** 325. 1962
Chimaphila	**42:** 61. 1961
Chiogenes = Gaultheria	
Chionanthus	**40:** 380. 1959
*Chrysobalanus	**51:** 523. 1970
Chrysophyllum	**41:** 10. 1960
*Chrysosplenium	**53:** 453. 1972
Cicca = Phyllanthus	
*Cichorium	**54:** 47. 1973
Cinnamomum	**39:** 334. 1958
Cissampelos	**45:** 33. 1964
Cissus	**46:** 54. 1965
Citrus	**43:** 17. 1962
Claytonia	**50:** 584. 1969
Cleome	**44:** 87. 1963
*Clethra	**42:** 103. 1961
Cliftonia	**42:** 101. 1961
*Clusia	**57:** 78. 1976
*Cnidoscolus	**48:** 349. 1967
*Coccoloba	**46:** 114. 1965
Coccolobis = Coccoloba	
*Cocculus	**45:** 30. 1964
Colocasia	**41:** 56. 1960
Colubrina	**45:** 455. 1964
*Comptonia	**52:** 315. 1971
Conocarpus	**45:** 298. 1964
*Conopholis	**52:** 420. 1971
Convolvulus	**41:** 308. 1960
Corchorus	**46:** 295. 1965
Corculum = Antigonon	
*Cornus	**47:** 109. 1966

Oxycoccus = Vaccinium
*Oxydendrum **42:** 56. 1961
Padus = Prunus
Panax **47:** 132. 1966
Papaver **43:** 330. 1962
Parageum = Geum
*Parietaria **52:** 64. 1971
Parkinsonia **57:** 32. 1976
Parnassia **53:** 461. 1972
Parsonsia = Cuphea
Parthenocissus **46:** 57. 1965
*Passiflora **42:** 211. 1961
Pedilanthus **48:** 427. 1967
Peiranisia = Cassia
*Peltandra **41:** 55. 1960
*Penthorum **53:** 419. 1972
Peplis **45:** 241. 1964
Persea **39:** 330. 1958
Persicaria = Polygonum
Phacelia **41:** 202. 1960
Pharbitis = Ipomoea
Phenianthus = Lonicera
*Philadelphus **53:** 480. 1972
Philoxerus: see Blutaparon
Phlox **41:** 207. 1960
*Phoradendron **63:** 407. 1982
*Phryma **53:** 227. 1972
Phyllanthus **48:** 332. 1967
*Physocarpus **55:** 316. 1974
Phytarrhiza = Tillandsia
Picramnia **43:** 181. 1962
Picris **54:** 67. 1973
*Pieris **42:** 51. 1961
*Pilea **52:** 55. 1971
Pilostaxis = Polygala
Piriqueta **42:** 206. 1961
*Pisonia **55:** 28. 1974
*Pistia **41:** 61. 1960
Pithecellobium **55:** 115. 1974
Pityothamnus = Asimina
Planera **51:** 31. 1970
Platanus **44:** 206. 1963
Pleuropterus = Polygonum
Plumbago **40:** 393. 1959
Podophyllum **45:** 13. 1964
*Podostemum **56:** 461. 1975
Poinciana = Caesalpinia
Poinsettia = Euphorbia
Polanisia = Cleome
Polemonium **41:** 210. 1960
Polycodium = Vaccinium
*Polygala **52:** 271. 1971
Polygonella **46:** 112. 1965
Polygonum **46:** 105. 1965
*Poncirus **43:** 14. 1962
*Porteranthus **55:** 329. 1974
*Portulaca **50:** 571. 1969
Portulacastrum = Trianthema
*Potamogeton **59:** 174. 1978
*Potentilla **55:** 373. 1974
Poterium = Sanguisorba
Pouteria **41:** 11. 1960
Prenanthes **54:** 76. 1973
Prinos = Ilex
*Proboscidea **58:** 33. 1977
*Prunus **55:** 654. 1974
Pseudo-elephantopus **63:** 505. 1982
Psidium **41:** 277. 1960
Psilorhegma = Cassia
Ptelea **43:** 9. 1962
Pyracantha **55:** 624. 1974
Pyrola **42:** 62. 1961
Pyrrhopappus **54:** 55. 1973
*Pyrus **55:** 640. 1974
*Pyxidanthera **40:** 166. 1959
Quamoclit = Ipomoea
*Quercus **52:** 179. 1971
Ramium = Boehmeria
Rapanea = Myrsine
Reynosia **45:** 461. 1964
Reynoutria = Polygonum
Rhacoma = Crossopetalum
Rhamnus **45:** 445. 1964
*Rhexia **63:** 432. 1982
*Rhizophora **45:** 286. 1964
Rhodiola = Sedum
*Rhododendron **42:** 30. 1961
Rhodomyrtus **41:** 278. 1960
Rhus **43:** 370. 1962
Rhytiglossa = Justicia
*Ribes **53:** 466. 1972
*Ricinus **48:** 379. 1967
Riedlea = Melochia
Rivea: see Turbina
Robertiella = Geranium
*Rosa **55:** 611. 1974
Rotala **45:** 240. 1964
Rubacer = Rubus
*Rubus **55:** 352. 1974
*Ruellia **51:** 285. 1970
Rufacer = Acer
Rugelia = Senecio
Rumex **46:** 99. 1965
*Ruppia **59:** 185. 1978
Ruta **43:** 5. 1962
*Sabatia **63:** 449. 1982

Tubiflora = Elytraria		*Wallia* = Juglans	
Tulipastrum = Magnolia		Waltheria	**47**: 72. 1966
Turbina	**41**: 316. 1960	Wolffia	**41**: 71. 1960
Turnera	**42**: 208. 1961	Wolffiella	**41**: 70. 1960
*Ulmus	**51**: 21. 1970	*Xanthoxalis* = Oxalis	
*Urtica	**52**: 47. 1971	*Xanthoxylum* = Zanthoxylum	
Urticastrum = Laportea		*Ximenia	**63**: 393. 1982
Vaccinium	**42**: 69. 1961	*Xolisma* = Lyonia	
Vachellia = Acacia		*Xylophylla* = Phyllanthus	
Valeriana	**46**: 220. 1965	*Xylosteon* = Lonicera	
Valerianella	**46**: 223. 1965	*Xyris	**64**: 428. 1983
Vernonia	**63**: 494. 1982	*Yeatsia* = Dicliptera	
Viburnum	**47**: 41. 1966	Youngia	**54**: 89. 1973
Viola	**42**: 324. 1961	Zanthoxylum	**43**: 6. 1962
Vitis	**46**: 61. 1965	*Zenobia	**42**: 45. 1961
*Voyria	**63**: 483. 1982	Ziziphus	**45**: 459. 1964
Waldsteinia	**55**: 388. 1974	*Zygophyllidium* = Euphorbia	

ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

The Generic Flora of the Southeastern United States is a long-term, comprehensive project covering the 192 families and approximately 1280 genera of seed-bearing plants of North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana, an area of some 444,000 square miles (1.15 million square kilometers). For each family and genus original observations are synthesized with published information from botanical and other journals of the world to show much of what is and is not known about each group. The treatment for each family and its genera includes descriptions, keys, original place of publication, principal synonyms, common names, number of species (and sometimes brief descriptions and distributions of these), infrafamilial and infrageneric ranks represented, relationships, diagnostic features, economic importance, and a wide variety of notes from all branches of botany. Descriptions are based primarily on the plants of the southeastern United States, but information about extraregional members of a family or genus is often included. Annotated references provide a summary of published information. Original, detailed illustrations show generic characteristics and various features of structure and biology.

In addition to the one hundred articles indexed above, there are fifty collateral papers and notes that have developed from this work. The 150 papers total 2664 pages. Four hundred and ninety plates illustrating 552 genera have been prepared, with one to twenty-seven plates for each of 179 families.

Initially begun through the generosity of George R. Cooley (see frontispiece and dedication of *Journal of the Arnold Arboretum,* Vol. 63, no. 4, 1982), work on the Generic Flora has also been supported by grants from the National Science Foundation. It is currently supported by BSR-8111520 (C. E. Wood, Jr., principal investigator), under which these indexes were prepared, and by BSR-8303100 (N. G. Miller, principal investigator).

A SYNOPSIS OF THE CHINESE SPECIES OF ASARUM (ARISTOLOCHIACEAE)

CHING-YUNG CHENG AND CHUN-SHU YANG

THE GENUS *Asarum* L. has its center of distribution in eastern Asia, especially in China and Japan. The genus includes two distinct subgenera, each with several subcategories. Subgenus ASARUM is characterized by almost distinct perianth lobes and more or less united styles with terminal stigmas, while subg. HETEROTROPA has an obvious floral tube and six free styles with lateral stigmas. Due to these and other differences, the genus has occasionally been divided into two, three, or even more segregate genera (e.g., *Hexastylis* Raf., *Heterotropa* Morren & Dcne., *Asiasarum* Maekawa, *Japonasarum* Nakai, and *Geotaenium* Maekawa). The characters utilized to distinguish these genera, however, are of comparatively minor significance. Since *Asarum* appears to be a natural and consistent taxon with close relationships among its species and salient evolutionary trends in its floral structures, it has been maintained by most authors (e.g., Braun, 1861; Hayata, 1915; Maekawa, 1932; Liu & Lai, 1976), as well as by the present ones. In this paper we divide *Asarum* into two subgenera and propose five sections and four series, essentially following Araki's (1937) hierarchy but with some emendations and modifications.

In China species of *Asarum* that produce pungent aromatic roots are used in traditional medicine as a remedy for pain and colds. Among them, *A. heterotropoides* var. *mandshuricum* is considered of the greatest value, although *A. sieboldii* is believed to have been the first species used in ancient Chinese medicine. All the remaining species, including those utilized in folk medicine, are used for the same or slightly different purposes.

CONSPECTUS OF THE GENUS ASARUM IN CHINA[1]

Asarum L. Sp. Pl. 442. 1753; Gen. Pl. ed. 5. 201. 1754. LECTOTYPE SPECIES: *A. europaeum* L., *fide* Britton & Brown, Ill. Fl. N. U. S. ed. 2. **1:** 642. 1913.

Hexastylis Raf. Neogenyton, 3. 1825. TYPE SPECIES: *H. arifolia* (Michx.) Raf., based on *Asarum arifolium* Michx. (U. S. A.)

Heterotropa Morren & Dcne. Ann. Sci. Nat. II. **2:** 314. *t. 10.* 1834. TYPE SPECIES: *H. asaroides* Morren & Dcne. (Japan.)

Japonasarum Nakai, Fl. Sylv. Koreana **21:** 16. 1936. TYPE SPECIES: *J. caulescens* (Maxim.) Nakai, based on *Asarum caulescens* Maxim. (Japan, Korea.)

Asiasarum Maekawa *in* Nakai, Fl. Sylv. Koreana **21:** 17. 1936. TYPE SPECIES: *A. sieboldii* (Miq.) Maekawa, based on *Asarum sieboldii* Miq. (Korea.)

Geotaenium Maekawa, Proc. VII Pacific Sci. Congr. **5:** 217. 1953. TYPE SPECIES: *G. epigynum* (Hayata) Maekawa, based on *Asarum epigynum* Hayata. (China, Taiwan.)

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[1] Some species occurring in Taiwan are not included in this treatment because we have not seen adequate material.

Journal of the Arnold Arboretum **64:** 565–597. October, 1983.

Perennial herbs; rhizomes short and oblique or long and prostrate; roots and rhizomes pungently aromatic. Leaves 1 or 2, usually long-petiolate, variously cordate or sagittate. Flowers solitary, axillary or between 2 opposite leaves, greenish, usually with tufts of short purplish hairs (rarely glabrous); peduncles usually short, with 1 or 2 cataphylls at base; perianth of 3 sepals, these separate or coalescent at base and forming a cupular, urceolate, campanulate, or funnelform tube, the tube often ridged or tessellate on inner surface and constricted at upper end to form orifice, the orifice usually with laminate ring; perianth lobes 3, erect, spreading, or reflexed; stamens 12 in 2 series, rarely with extra whorl of 3 aberrant stamens or staminodes, filaments evident or anthers subsessile; ovary inferior or half inferior (sometimes nearly superior), 6-loculate, the placentation axile with numerous ovules, the styles 6, distinct with essentially terminal stigmas or united and with lateral stigmas. Fruit a fleshy, berrylike capsule, splitting irregularly when ripe; seeds numerous, more or less cordate, convex dorsally, plane or grooved ventrally, arillate at base. $2n = 12$, 24, 26.

About ninety species, mostly in the warm-temperate region of eastern Asia; a few species in North America and one endemic to Europe. Thirty-one species, three varieties, and one form occur in China and are distributed mainly along the Yangtze River. A key to the subgenera, sections, and series into which these species fall is presented below.

KEY TO THE SUBGENERA, SECTIONS, AND SERIES OF ASARUM

1. Perianth with lobes essentially free above ovary, not forming distinct tube or only very short one; stamens with ± long filaments; styles united into column, the 6 stigmas radiating, essentially terminal (subg. ASARUM).
    2. Perianth with tube completely lacking, the lobes free, erect or rarely reflexed (sect. ASARUM).
        3. Perianth lobes erect, caudate or pointed. . . . . ser. Calidasarum.
        3. Perianth lobes reflexed, neither caudate nor long-pointed. . . . . ser. Japonasarum.
    2. Perianth with tube very short; the lobes united at very base, erect or reflexed. . . . . sect. BREVITUBA.
1. Perianth with lobes united above ovary, forming tube of various shapes; stamens subsessile or with very short filaments, if with long filaments then inserted on ovary; styles 6, free or rarely united basally, often bifid at apex, stigmas lateral or rarely ± terminal (subg. HETEROTROPA).
    4. Stamens inserted on ovary, filaments longer than anthers; ovary often half inferior, styles short; perianth smooth throughout, orifice lacking laminate ring. . . . . sect. ASIASARUM.
    4. Stamens not inserted on ovary, filaments usually very short; ovary inferior or half inferior, rarely almost superior, styles long; perianth with lobes often with papillate or pulvinate areas at base, orifice usually with laminate ring.
        5. Perianth with tube usually 1–4 cm long, often with conspicuous orifice ring, papillate area localized at base of lobes (sect. HETEROTROPA).
            6. Styles not bifid at apex, stigmas terminal or subterminal. . . . . ser. Achidasarum.
            6. Styles bifid at apex, stigmas lateral. . . . . ser. Bicorne.
        5. Perianth with tube usually 5–8 cm long, orifice lacking evident ring, papillae scattered from middle of lobes downward into tube and arranged in vertical rows. . . . . sect. LONGIFLORA.

SUBGENUS ASARUM

Asarum subg. **Asarum**

Asarum subg. *Choridasarum* Araki, Acta Phytotax. Geobot. **6:** 125. 1937.

Perianth lobes free or united only at base and forming very short tube; stamens with filaments usually longer than anthers; styles united into column, 6-lobed at apex, stigmas mostly terminal. TYPE SPECIES: *A. europaeum* L.

Nine species and one variety in two sections and two series in China.

Key to the Species of *Asarum* subg. ASARUM

1. Perianth lobes totally free, erect or reflexed, not forming tube.
    2. Perianth lobes erect and caudate or long-pointed.
        3. Perianth lobes with abrupt tail ca. 1 cm long; lobes of styles entire, stigmas terminal.
            4. Leaves broadly ovate, triangular-ovate, or ovate-cordate, green and mostly without white blotches above. .... 1. *A. caudigerum.*
            4. Leaves mostly subcordate or broadly ovate, with minute, densely spaced white blotches above. .... 1a. *A. caudigerum* var. *cardiophyllum.*
        3. Perianth lobes gradually tapering into long point to 1 cm long; lobes of styles notched, with stigmas at base of notches. .... 2. *A. renicordatum.*
    2. Perianth lobes reflexed, with apex acute or obtuse, never caudate or long-pointed; leaves usually 2 to 4, apparently opposite.
        5. Plants densely covered with long, white hairs (black when dry); stamens and styles not exserted, stigmas terminal; leaves broadly ovate, acute or short-acuminate. .... 3. *A. pulchellum.*
        5. Plants sparingly pubescent; stamens and styles often exserted; lobes of styles notched, stigmas outside of notches; leaves cordate, acuminate. .... 4. *A. caulescens.*
1. Perianth lobes united at base, forming very short tube above ovary.
    6. Perianth lobes with short tail 1–4 mm long; leaves pubescent only along veins.
        7. Plants 20–30 cm high; perianth lobes with incurved tail ca. 2 mm long; stamens 12, connectives elongated and ligulelike. ....5. *A. caudigerellum.*
        7. Plants 10–15 cm high; perianth lobes acute or, if short-tailed, tail not incurved; stamens 12 or fewer, connectives not elongated. .... 6. *A. debile.*
    6. Perianth lobes not tailed; leaves usually with scattered pubescence on lower surface.
        8. Perianth lobes reflexed; styles slender, stigmas not radiating downward; peduncles long and filiform. .... 7. *A. himalaicum.*
        8. Perianth lobes erect or spreading; styles short and thick, stigmas radiating downward; peduncles rather stout, never filiform.
            9. Leaves cordate or broadly ovate; ovary broadly ovoid, with 6 pronounced ribs; mainland China. .... 8. *A. geophyllum.*
            9. Leaves narrowly ovate or triangular-ovate; ovary narrowly obovoid, lacking ribs; Taiwan and Hainan. .... 9. *A. epigynum.*

Asarum sect. **Asarum**

Asarum sect. *Euasarum* Braun, Index Sem. Berol. Append. 12. 1861.
Asarum sect. *Ceratasarum* Braun, *ibid.*

Perianth lobes essentially free, not forming true tube.

Asarum sect. ASARUM comprises two series with four species and one variety in China.

Asarum ser. **Calidasarum** (Araki) C. Y. Cheng & C. S. Yang, stat. nov.

Asarum sect. *Calidasarum* Araki, Acta Phytotax. Geobot. **6:** 125. 1937.

Perianth lobes erect, long-pointed to caudate at apex. TYPE SPECIES: *Asarum leptophyllum* Hayata (= *A. caudigerum* Hance).

Two species and one variety in China.

1. **Asarum caudigerum** Hance, London Jour. Bot. **19:** 142. 1881; Hemsley *in* Curtis's Bot. Mag. **116:** *t. 7126.* 1890. TYPE: Guangdong, East River, *Hance 21336* (n.v., photo PE[2]).

Asarum leptophyllum Hayata, Ic. Pl. Formosa. **5:** 147. 1915. TYPE: Taiwan, Arisan, *Hayata & Ito s.n.* (photo PE).
Asarum leptophyllum var. *triangulare* Hayata, *ibid.* TYPE: Taiwan, "Arisan," *Ito & Hayata s.n.* (photo PE).

DISTRIBUTION. Zhejiang, Jiangxi, Fujian, Taiwan, Hubei, Hunan, Guangdong, Guangxi, Sichuan, Guizhou, and Yunnan. Thickets along streams and roadsides; frequently at 350–1160 m alt.

Hayata described *Asarum leptophyllum* from Taiwan in 1915. He stated that it is allied with *A. caudigerum* Hance and is distinguished only in having light green flowers instead of reddish ones. He also considered plants with triangular leaves to constitute var. *triangulare.* In fact, the reddish flowers of *Asarum* are due to the presence of reddish hairs on the otherwise greenish perianth lobes. Both the amount of pubescence and the shape of the leaves are variable on individual plants. Based on comparisons of material from Fujian with the figures presented by Liu and Lai (1976), we cannot support the separation of these three taxa.

1a. **Asarum caudigerum** Hance var. **cardiophyllum** (Franchet) C. Y. Cheng & C. S. Yang, comb. et stat. nov.

BASIONYM: *Asarum cardiophyllum* Franchet, Bull. Mus. Hist. Nat. Paris **1:** 66. 1895. SYNTYPES: Yunnan, Long-ki, *Delavay 5150* (photo PE), *5205* (n.v.).

According to Franchet, *Asarum cardiophyllum* is closely related to *A. caudigerum* Hance, differing in having floral stems that bear four leaves in two pairs, and styles that are united into an undivided column. These features, however, also occur in typical *A. caudigerum.* Since plants of *A. cardiophyllum* from Sichuan and northern Yunnan have mainly cordate leaves, usually with

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[2] Acronyms for herbaria follow those outlined by Holmgren, Keuken, & Schofield in *Index Herbariorum,* ed. 7. 1981 (Regnum Vegetabile **106**), with the following exceptions (all located in the People's Republic of China) that do not appear in that work: AHU, Anhui University, Hefei, Anhui; GIM, Guizhou Institute of Chinese Traditional Medicine, Guiyang, Guizhou; HIM, Hangzhou Institute of Materia Medica, Zhejiang Academy of Experimental Sanitary Sciences, Hangzhou, Zhejiang; OTS, Sichuan School of Chinese Traditional Medicine, Omei, Sichuan; PTM, Beijing Chinese Traditional Medicinal College, Beijing; and SIT, Sichuan Institute of Chinese Traditional Medicine, Chongqing, Sichuan.

fine white patches on the upper surface, we feel that these plants are best accorded varietal status under *A. caudigerum*.

2. **Asarum renicordatum** C. Y. Cheng & C. S. Yang, sp. nov. FIGURE 1.

Proximum A. caudigero, sed foliis renicordatis, lobis perianthii apice longe attenuatis, lobis stigmatis obcordatis, differt.

Acaulescent perennial herbs from long, slender rhizomes. Leaves 2, opposite; petiole 10–14 cm long; blade renicordate or subcordate, 3–4 by 6–7.5 cm, rounded and obtuse (rarely acute) at apex, with scattered hairs above, more densely pubescent below, margin densely ciliate. Flowers solitary between leaves; peduncle ca. 2.5 cm long, densely pubescent; perianth campanulate, yellowish brown-hairy outside, the lobes slightly united at base but not forming tube, triangular-lanceolate, ca. 10 by 4 mm, usually attenuated into point 4–10 mm long at apex; stamens with filaments ca. 1 mm long, connectives awl shaped; styles united and 6-lobed at apex, the lobes notched, ± inverted heart-shaped, the stigmas attached at notches. Fruits not seen.

TYPE. Anhui, Huang-shan, mountain slope near stream, *Nanjing Pharmacy College s.n.* (holotype, PTM; isotype, PEM).

ADDITIONAL SPECIMEN EXAMINED. **Anhui:** Jui-hua-shan, 720 m alt., *An 5583* (AHU).

Asarum renicordatum is closely related to *A. caudigerum* Hance, but differs in having renicordate leaves, perianth lobes with gradually tapering, long-pointed apices, and notched style tips. While its leaves are similar to those of *A. forbesii* Hance, its flowers differ considerably. The specific name is derived from the broad, kidney-shaped leaves of the plants.

Asarum ser. **Japonasarum** (Nakai) C. Y. Cheng & C. S. Yang, stat. nov.

Japonasarum Nakai, Fl. Sylv. Koreana **21:** 16. 1936.
Asarum sect. *Japonasarum* (Nakai) Araki, Acta Phytotax. Geobot. **7:** 125. 1937.

Perianth lobes reflexed downward. TYPE SPECIES: *Japonasarum caulescens* (Maxim.) Nakai (= *Asarum caulescens* Maxim.).

Two species in China, others in Japan and Korea.

3. **Asarum pulchellum** Hemsley, Gard. Chron. III. **7:** 422. 1890; Jour. Linn. Soc. **26:** 360. 1891. TYPE: Hubei, *Henry 7800* (photo PE).

DISTRIBUTION. Anhui, Jiangxi, Hubei, Sichuan, and Guizhou. In woods in mountainous areas, often in loamy soil; abundant at 700–1700 m alt.

This species is easily distinguished from near allies by its dense, long, white hairs, which become black when dry.

4. **Asarum caulescens** Maxim. Bull. Acad. Sci. St.-Pétersb. **17:** 162. 1872. TYPE: Japan, *Tschonoski s.n.* (photo of syntype PE).

Asarum caulescens var. *setchuenense* Franchet, Jour. Bot. Morot **12:** 302. 1898. Type: SICHUAN, Tchen keou tin, *Farges s.n.* (n.v.).

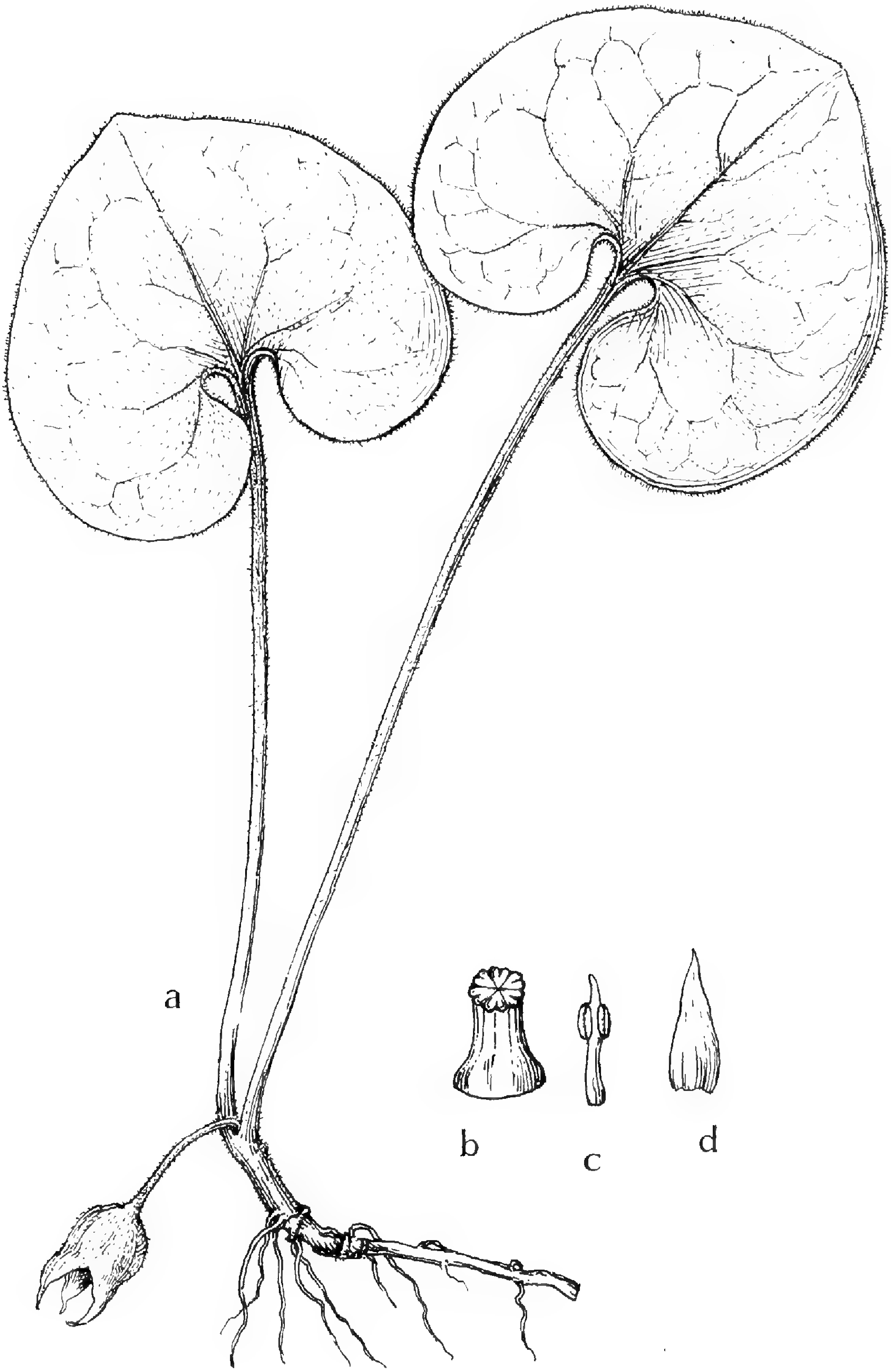

FIGURE 1. **Asarum renicordatum:** a, habit of flowering plant, × .8; b, styles and radiating stigmas, × 1.6; c, anther, × 1.6; d, perianth lobe, × 1.6.

Asarum franchetianum Diels, Bot. Jahrb. **29:** 308. 1901. TYPE: Sichuan, Nanchuan, *Bock von Rosthorn 2446* (photo PE).
Japonasarum caulescens (Maxim.) Nakai, Fl. Sylv. Koreana **21:** 17. 1936.

DISTRIBUTION. Shaanxi, Gansu, Hubei, Sichuan, and Guizhou.

This species was first described from Japan. It has not been found in the eastern provinces of China, although it has often been collected in western China. This discontinuous distribution caused Franchet to distinguish the Chinese plant as *Asarum caulescens* var. *setchuenense,* and he even contemplated recognizing it as an independent species. Franchet distinguished the Chinese plants on the basis of their cordate style lobes and their stamens that are slightly shorter than the stylar column. However, dissections of flowers from Japanese specimens and comparisons with dissections of Chinese specimens (including plants from Sichuan, Hubei, and Shaanxi) indicate few if any differences between the Japanese and Chinese plants. Consequently, we include var. *setchuenense* in synonymy. With regard to *Asarum franchetianum,* Diels pointed out that the perianth tube is adnate to the ovary only halfway in the Japanese plant, while in the plants from Sichuan the adnation is almost complete. However, if the overall similarity of floral morphology is considered, *A. franchetianum* seems inseparable from *A. caulescens.*

Asarum sect. **Brevituba** C. Y. Cheng & C. S. Yang, sect. nov.

Perianthium lobis basi coalescentibus et tubo brevi. TYPE SPECIES: *Asarum himalaicum* Hooker f. & Thomson.

Four or perhaps five species in China.

5. **Asarum caudigerellum** C. Y. Cheng & C. S. Yang, sp. nov. FIGURE 2.

Species A. debili similis laminis foliorum in medio margineque leviter incurvatis, base perianthiis breve tubularibus et lobis in apicem brevissime caudatis, differt plantis altioribus. foliis apice acuminatis vel longe acuminatis, connectivis antherarum apice valde productis, longe ligulatis.

Perennial herbs, 20–40 cm high; rhizomes long and horizontal with prolonged internodes; stems 2–5 cm long, inclined at tip, with 1 or 2 pairs of opposite leaves. Leaves with petiole 4–18 cm long, the cataphylls at its base broadly ovate, ca. 2 by 1–1.5 cm, densely ciliate; blade cordate or oblong-cordate, 3–7 by 4–10 cm, acuminate or long-acuminate at apex, slightly incurved at margin, cordate at base. Flowers dark purple; peduncle 1–1.5 cm long; perianth with the tube very short, ca. 5 mm long, 10 mm in diameter, the lobes triangular-ovate, 10 by 7 mm, acuminate with incurved tail ca. 5 mm long, pilose on outer surface; stamens with filaments usually longer than anthers; ovary inferior, subspherical, 6-ribbed, pilose, the styles united, with 6 short radiating branches at apex.

TYPE. Sichuan, Mt. Omei, between 1700 and 2100 m alt., under thickets, along mountain path, *K. H. Yang 54370* (PE).

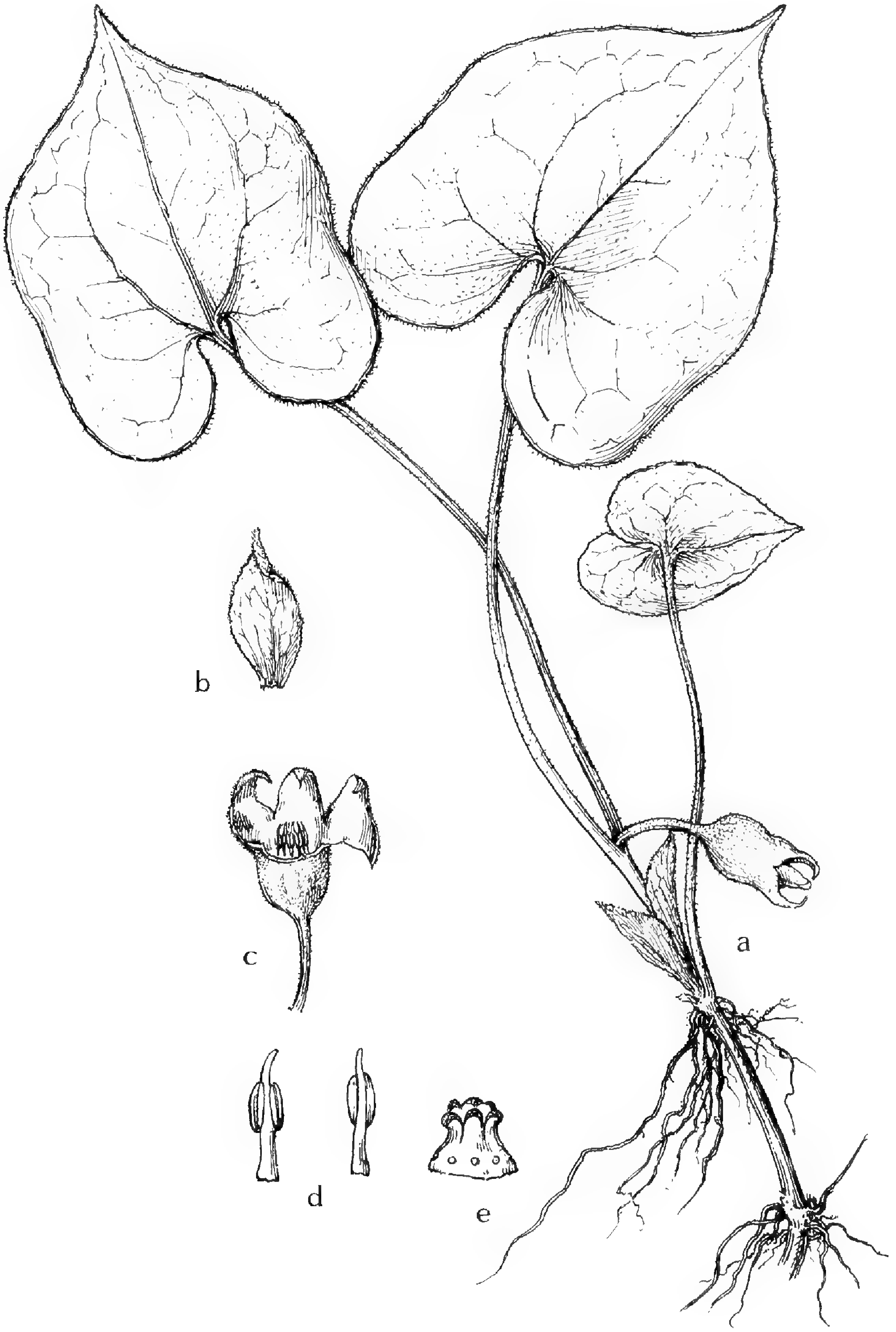

FIGURE 2. **Asarum caudigerellum:** a, habit of flowering plant, × .65; b, cataphyll, × 1.3; c, flower, with perianth lobe cut to expose stamens, × 1; d, stamens, × 1.3; e, stylar column, showing coherent portion and terminal stigmas, × 1.3.

ADDITIONAL SPECIMENS EXAMINED. **Sichuan:** Mt. Omei, 1900 m alt., *C. Y. Cheng 807a* (PEM); Nanchuan, *J. H. Xung 90302* (PE); Beichuan, *Econ. Exped. 505* (SIT); Tien-quan, *H. L. Tsiang 34001* (SZ). **Hubei:** He-feng, *H. J. Li 8487* (PTM); Xuan-en, *H. J. Li 3989* (PTM). **Guizhou:** Na-yung, *Bi-jieh Exped. 420* (PE). **Yunnan:** I-liang, *H. T. Tsai 52083* (PE).

Asarum caudigerellum is closely related to *A. debile* Franchet but differs in having a larger stature; acuminate leaves; and 12 stamens, all of which are normally developed, produce viable pollen, and have anther connectives with long-produced tips. *Asarum debile,* on the other hand, is a small, weak plant with acute leaves, 12 or usually fewer stamens, and anther connectives that are not produced.

The specific name, a diminutive of *caudigerum,* refers to the short tail on the perianth lobes.

6. **Asarum debile** Franchet, Jour. Bot. Morot **12:** 305. 1898. TYPE: Sichuan, Cheng-kou, *Farges s.n.* (P, n.v.).

DISTRIBUTION. Anhui, Shaanxi, Hubei, and Sichuan. Found occasionally in rocky, moist places near streams; 1300–2300 m alt.

7. **Asarum himalaicum** Hooker f. & Thomson ex Klotzsch, Monatsber. Deutsch. Akad. Wiss. Berlin **1:** 385. 1859; Duchartre *in* DC. Prodr. **15:** 424. 1864; Hooker f. Fl. Brit. India **5:** 72. 1890. TYPE: Sikkim Himalaya, *J. D. Hooker s.n.* (K).

DISTRIBUTION. Shaanxi, Gansu, Hubei, Sichuan, Guizhou, Yunnan, and Xizang; also in India. Near streams and under thickets in shady, moist places.

8. **Asarum geophyllum** Hemsley, Gard. Chron. III. **7:** 422. 1890; Hooker f. Curtis's Bot. Mag. **117:** *t. 7168.* 1891. TYPE: Guangdong, "North River," *Ford 125* (photo PE).

Asarum cavaleriei Lévl. Repert. Sp. Nov. **9:** 78. 1910. TYPE: Guizhou, "Lofou," *Cavalérie 3671* (K, n.v., photo PE).

DISTRIBUTION. Guizhou, Guangxi, and Guangdong. In shady forests or moist valleys; 250–700 m alt.

9. **Asarum epigynum** Hayata, Ic. Pl. Formosa. **5:** 140. 1915; Liu & Lai *in* Li, Fl. Taiwan **2:** 557. 1976; Maekawa, Jour. Jap. Bot. **52:** 231. 1977. TYPE: Taiwan, without precise locality, *T. Soma s.n.* (n.v.).

Geotaenium epigynum (Hayata) Maekawa, Proc. VII Pacific Sci. Congr. **5:** 219. 1953; Jour. Jap. Bot. **52:** 251. 1977; *ibid.* **53:** 291. 1978.

DISTRIBUTION. Taiwan and Hainan. In moist valleys and forests.

Maekawa removed this species from *Asarum* and placed it in the genus *Geotaenium* on the basis of the plant's chromosome number ($2n = 12$) and its flowers with a rudimentary "corolla." Otherwise, this species is a typical *Asa-*

rum, and its floral structure suggests a close relationship with *A. geophyllum.* The rudimentary "petals" appear to be staminodia, and staminodia are also present in the flowers of *A. macranthum* (Maekawa, 1978). An extra whorl of aberrant stamens has also been reported in the flowers of *A. caudigerum* of the same subgenus.

SUBGENUS HETEROTROPA

Asarum subg. **Heterotropa** (Morren & Dcne.) Schmidt *in* Engler & Prantl, Nat. Pflanzenfam. ed. 2. **16b:** 230. 1935. *Heterotropa* Morren & Dcne. Ann. Sci. Nat. II. **2:** 314. *t. 10.* 1834.

Asarum subg. *Gamoasarum* Araki, Acta Phytotax. Geobot. **6:** 125. 1937.

Perianth lobes united above ovary, forming variously shaped perianth tubes; stamens with very short filaments or subsessile; styles often free, rarely short and subconnate (in Japanese species), often bifid at apex, rarely subentire. TYPE SPECIES: *Heterotropa asaroides* Morren & Dcne. (= *Asarum asaroides* (Morren & Dcne.) Makino).

Twenty-two species, three varieties, and one form in China, these falling into three sections and two series.

Key to the Species of *Asarum* Subg. HETEROTROPA

1. Stamens with filaments evident, longer than anthers; ovary half inferior; styles short; perianth with the tube naked at throat, lacking papillae and ring, the lobes smooth at base, lacking papillae or pulvinate areas.
    2. Perianth lobes erect or spreading, never reflexed at anthesis; leaves short-acuminate, with scattered hairs over upper surface.
        3. Leaves usually hairy only on veins on lower surface, petiole glabrous. . . . . 10. *A. sieboldii.*
        3. Leaves usually densely pubescent on lower surface, petiole pubescent. . . . . 10a. *A. sieboldii* f. *seoulense.*
    2. Perianth lobes reflexed at anthesis; leaves acute or blunt at apex, short-pubescent on veins above. . . . . 11. *A. heterotropoides* var. *mandshuricum.*
1. Stamens with filaments shorter than anthers; ovary inferior or half inferior, occasionally nearly superior, styles rather long; perianth having tube with (rarely without) orifice ring at throat, lobes papillate or pulvinate at base.
    4. Styles not bifid at apex, stigmas terminal or subterminal.
        5. Perianth having the tube with orifice ring, inner surface tessellate with slightly elevated bars (rarely longitudinally ridged), the lobes not reflexed, usually papillate near base.
            6. Rhizomes long and slender, mostly creeping; leaves elliptic-ovate, acuminate; perianth tube gradually dilated above orifice, forming neck, then divided into lobes. . . . . 12. *A. chinense.*
            6. Rhizomes short and thick, erect; leaves cordate or variously ovate, obtuse; perianth tube without neck, divided immediately into lobes. . . . . 13. *A. ichangense.*
        5. Perianth with the tube lacking orifice ring, inner surface longitudinally ridged, the lobes strongly reflexed laterally, pulvinate at base. . . . . 14. *A. fukienense.*
    4. Styles bifid at apex, stigmas attached laterally just below fork.
        7. Perianth having the tube generally urceolate with conspicuous constriction at

throat, usually with ring, inner walls longitudinally ridged or tessellate, the lobes papillate or pulvinate at base.

8. Perianth tube tessellate on inner surface.
    9. Perianth tube only slightly constricted at throat, orifice ring narrow.
        10. Perianth tube broad, cup shaped or hemispherical, the orifice large, ca. 1.5 cm in diameter, ring inconspicuous or very narrow; leaves with white patches on upper surface. .... 15. *A. chingchengense.*
        10. Perianth tube narrow, obconical, campanulate or cylindrical, the orifice small, 4–5 mm in diameter, ring conspicuous.
            11. Flowers ca. 10 mm in diameter; perianth with the tube cylindrical or campanulate, the lobes broad-ovate, ca. 5 mm long, without papillae at base. .... 16. *A. forbesii.*
            11. Flowers 20–30 mm in diameter; perianth with the tube obconical, the lobes triangular or triangular-ovate, 10–15 mm wide, with papillate area at base.
                12. Leaves ovate, 4–5 by 3–4 cm, usually light green beneath; cataphylls ovate, 1 cm long; perianth lobes with densely papillate area at base. .... 17. *A. taitonense.*
                12. Leaves broad-ovate or triangular-ovate, 8–10 by 7–9 cm, purplish beneath; cataphylls long, narrowly ovate, ca. 7 mm long; perianth lobes with only scattered papillae. .. .. 18. *A. infrapurpureum.*
    9. Perianth tube strongly constricted at throat, orifice ring broad and evident.
        13. Stigmas elongated, each extending along notch of bifid style and ± hooked at free end.
            14. Leaves triangular-ovate, veins reddish beneath, petiole streaked reddish brown; stamens oblong, anther connectives thick and bilobed at apex; stigmas elongated, decidedly hooked. .... 19. *A. macranthum.*
            14. Leaves ovate-cordate or narrowly ovate, the veins green beneath, the petiole green, not streaked; stamens triangular, anther connectives not bilobed at apex; stigmas oblong-ovoid, slightly hooked. .... 20. *A. crispulatum.*
        13. Stigmas ± ovoid, neither elongated nor hooked.
            15. Flowers to 5 cm in diameter; perianth with the tube subcylindrical, orifice ring 2–3 mm wide, the lobes broad-ovate, ca. 3 by 3–4 cm; leaves large, 7–15 by 6–11 cm. . . 21. *A. delavayi.*
            15. Flowers to 2.5 cm in diameter; perianth with the tube urceolate, orifice ring ca. 1 mm wide, the lobes broad- or triangular-ovate, ca. 8 by 8–12 mm; leaves 6–10 by 5–7 cm.
                16. Leaves dull green, white blotched above, purplish red below; anther connectives pointed. .... 22. *A. porphyronotum.*
                16. Leaves deep, lustrous green and not blotched white above, light green below; anther connectives rounded. .... 22a. *A. porphyronotum* var. *atrovirens.*
8. Perianth tube longitudinally ridged on inner surface, cross bars lacking or very faintly developed.
    17. Perianth tube swollen toward middle or apex, forming barrel-shaped or girdlelike dilated zone.
        18. Perianth with the lobes having pinkish, triangular, papillate area at base, the tube having dilated zone broad and near apex, inner surface with longitudinal ridges ca. 0.5 mm apart, orifice with narrow ring. .... 23. *A. inflatum.*

18. Perianth with the lobes having white or yellowish, circular or semicircular pulvinate area at base, the tube having inner surface of dilated zone without ridges, orifice ring absent.
    19. Perianth having the lobes with transverse rows of papillae below pulvinate area, the tube with dilated zone at middle and girdlelike, and with orifice large, ca. 1 cm in diameter; pedicels 1–5 cm long. .... 24. *A. maximum.*
    19. Perianth with the lobes lacking transverse rows of papillae below pulvinate area, the tube with dilated zone near apex, orifice small; pedicels ca. 9 cm long. .... 25. *A. insigne.*

17. Perianth tube enlarged gradually, not forming prominent dilated zone.
    20. Perianth tube and lower leaf surface glabrous.
        21. Perianth having the tube constricted slightly at throat, lacking orifice ring, the lobes with insignificant area of papillae. ... . 26. *A. nanchuanense.*
        21. Perianth having the tube constricted deeply at throat, with conspicuous orifice ring, the lobes with prominent papillate area at base.
            22. Robust plants with short rhizomes and ± thick, fleshy roots; leaves narrowly to broadly ovate, or hastate-oblong, 15–25 by 11–14 cm; flowers usually 2; anther connectives pointed. .... 27. *A. sagittarioides.*
            22. Slender plants with long rhizomes and fibrous, rarely ± fleshy roots; leaves cordate or narrowly elliptic-ovate, 8–14 by 5–8 cm; flowers usually solitary; anther connectives ligulate. .... 28. *A. longerhizomatosum.*
    20. Perianth tube and lower leaf surface densely pubescent with yellowish hairs. .... 29. *A. wulingense.*

7. Perianth with the tube funnelform, not constricted at throat or only slightly so, lacking orifice ring but occasionally with ring of papillae, the lobes with papillae at base usually large and scattered, sometimes in vertical rows and extending downward into tube.
    23. Perianth tube erect and symmetrical; leaves triangular-ovate or elliptic-ovate, acute or short-acuminate; rhizomes short, erect.
        24. Perianth tube 3–5 cm long, not much widened above; leaves triangular-ovate or subtriangular, the upper surface with whitish blotches, pubescent only on veins. .... 30. *A. magnificum.*
        24. Perianth tube ca. 1 cm long, widened from middle; leaves elliptic-ovate, the upper surface sparingly pubescent, not white blotched. .. .. 30a. *A. magnificum* var. *dinghuense.*
    23. Perianth tube often inclined to one side (slightly constricted at throat), slightly asymmetric; leaves narrowly ovate, triangular-ovate, or oblong-hastate, long-acuminate; rhizomes to 20 cm long, horizontal. .... 31. *A. petelotii.*

Asarum sect. **Asiasarum** (Maekawa) Araki, Acta Phytotax. Geobot. **6:** 126. 1937.

Asiasarum Maekawa *in* Nakai, Fl. Sylv. Koreana **21:** 17. 1936.

Perianth with tube lacking orifice ring, lobes smooth throughout; stamens inserted on surface of ovary, with long filaments. TYPE SPECIES: *Asarum sieboldii* Miq. (Japan).

Two species and one variety in China.

10. **Asarum sieboldii** Miq. Ann. Mus. Bot. Lugduno-Batavum **2:** 134. 1865. Type: Japan, Yezo, *Siebold s.n.* (L, n.v.).

Asiasarum sieboldii (Miq.) Maekawa *in* Nakai, Fl. Sylv. Koreana **21:** 22. 1936.

Distribution. Shandong, Henan, Shaanxi, Anhui, Zhejiang, Jiangxi, Hubei, and Sichuan; also in Korea and Japan. Moist soil in forested areas; 1200–2100 m alt.

10a. **Asarum sieboldii** Miq. f. **seoulense** (Nakai) C. Y. Cheng & C. S. Yang, stat. nov.

Basionym: *Asarum sieboldii* Miq. var. *seoulense* Nakai, Repert. Sp. Nov. **13:** 267. 1914; Bot. Mag. Tokyo **28:** 519. 1914. Type: Korea, Mt. Peukansan, *N. Okada s.n.* (TI?, n.v.).

Asiasarum heterotropoides Schmidt var. *seoulense* (Nakai) Maekawa *in* Nakai, Fl. Sylv. Koreana **21:** 20. 1936.

Distribution. Liaoning, Jilin, and extending northward into Korea. Habitat similar to that of the typical form.

Nakai compared the Korean plant with *Asarum sieboldii* and established var. *seoulense* on the basis of the dense pubescence on the lower leaf surface. This character, however, does not seem sufficient to warrant varietal status, and we think that the taxon is better recognized at the rank of forma.

11. **Asarum heterotropoides** Schmidt var. **mandshuricum** (Maxim.) Kitagawa, Lineam. Fl. Manshur. 174. 1939.

Asarum sieboldii var. *mandshuricum* Maxim. Mélanges Biol. Bull. Phys.-Math. Acad. Sci. St.-Pétersb. **8:** 399. 1871. Type: S Manchuria, without collector or number (LE, *n.v.*).

Asiasarum heterotropoides (Schmidt) Maekawa var. *mandshuricum* (Maxim.) Maekawa *in* Nakai, Fl. Sylv. Koreana **21:** 18. 1936.

Distribution. Heilongjiang, Jilin, and Liaoning; occasionally cultivated in the southern provinces. Moist, cool, shady forests.

Asarum sect. **Heterotropa** (Morren & Dcne.) Braun, Index Sem. Hort. Bot. Berol. Append. 13. 1861.

Heterotropa sect. *Circinaria* Maekawa, Jour. Jap. Bot. **57:** 262. 1982.

Perianth tubes variously shaped, usually with orifice ring; stamens subsessile or with very short filaments, never inserted on surface of ovary. Type species: *Asarum asaroides* (Morren & Dcne.) Makino.

Eighteen species and one variety in China, these falling into two series.

Asarum ser. **Achidasarum** (Duchartre) C. Y. Cheng & C. S. Yang, stat. nov.

Asarum sect. *Achidasarum* Duchartre *in* DC. Prodr. **15:** 426. 1864.

Styles entire at apex, stigmas terminal. Type species: *Asarum elegans* Duchartre = *A. parviflorum* (Hooker f.) Regel (Japan, Yokohama).

A small series comprising three species in China.

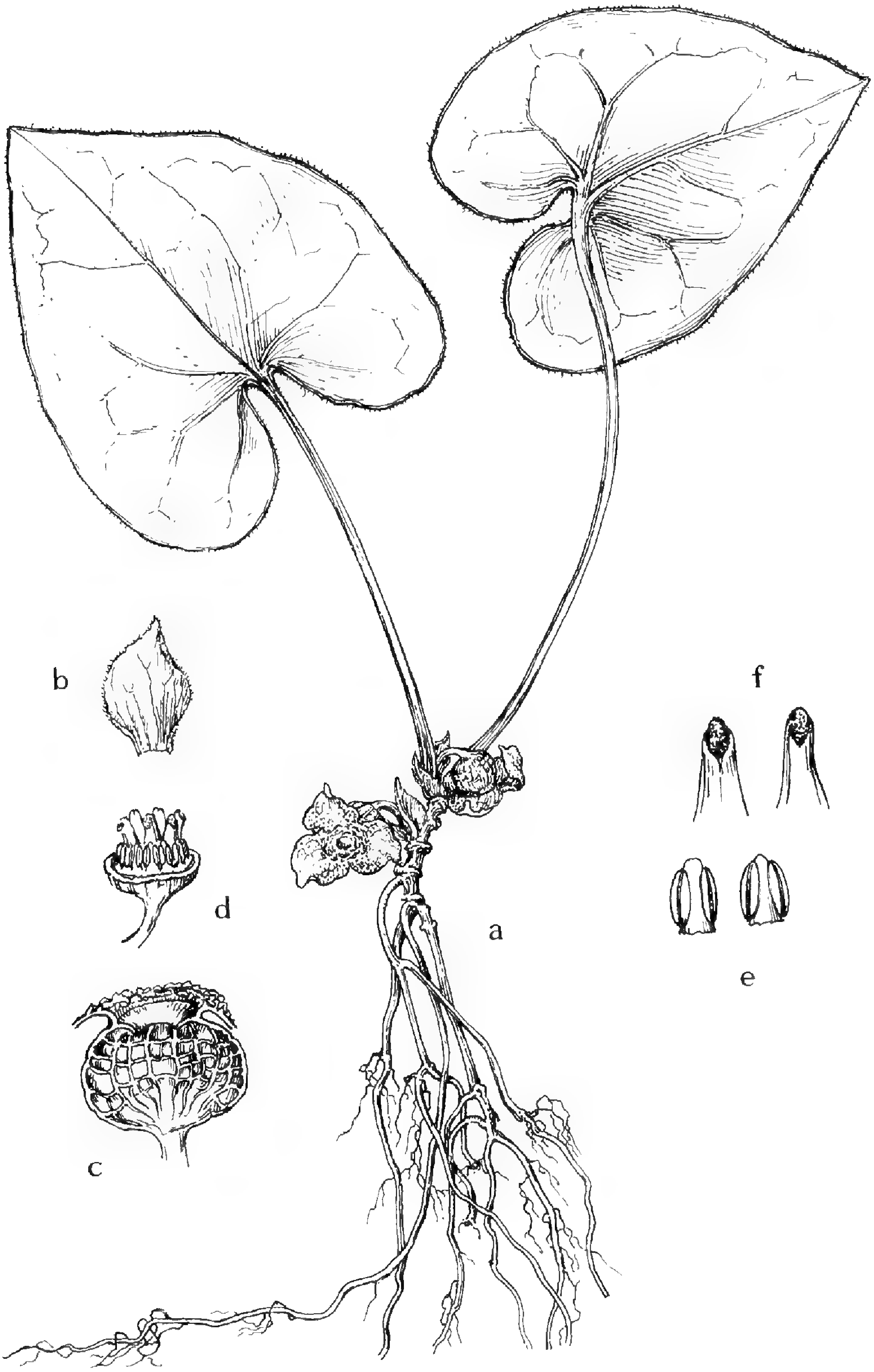

FIGURE 3. **Asarum ichangense**: a, habit of flowering plant, × .65; b, cataphyll, × 1.3; c, longitudinal section of perianth tube, showing tessellate inner surface and broad orifice ring, × 2.6; d, flower with perianth tube removed to show androecium and gynoecium, × 1; e, stamens, × 1.3; f, apex of styles, with terminal stigmas, × 2.

12. **Asarum chinense** Franchet, Jour. Bot. Morot **12:** 303. 1898. Type: Sichuan, Cheng-kou, *Farges 1205* (P, n.v., photo PE).

Asarum fargesii Franchet, Jour. Bot. Morot **12:** 306. 1898. Type: Sichuan, Cheng-kou, *Farges 966* (P, n.v., photo PE).

Distribution. Hubei and Sichuan. In forested ravines; 1300–1500 m alt.

Both *Asarum fargesii* and *A. chinense* were described by Franchet from material collected at Cheng-kou in northern Sichuan Province. During a special trip to the type locality of these two species to observe these plants in the field, we found that the criteria used by Franchet to distinguish plants of the two species (leaf coloration and the internal structure of the perianth tubes) do not hold. We have therefore placed *A. fargesii* in the synonymy of *A. chinense.*

13. **Asarum ichangense** C. Y. Cheng & C. S. Yang, sp. nov. Figure 3.

Affine A. chinensi, sed rhizomatis brevioribus, foliis cordatis vel ovato-cordatis apice obtusis, tubo perianthii valde constricto ad orem haud constricto ad collum, differt.

Perennial herbs from short, nearly perpendicular rhizomes. Leaves with petiole 3–15 cm long, the cataphylls at its base ovate or narrowly ovate, ca. 1 cm long, ciliate; blade cordate or cordate-ovate (rarely hastate), 3–6 by 3.5–7.5 cm, obtuse or acute at apex, cordate at base, usually dark green or rarely with white patches along midvein above, shortly pubescent along veins above, glabrous below. Flowers purplish green to dark purple, 1–1.5 cm in diameter; peduncle ca. 1 cm long, recurved; perianth with the tube spherical, ca. 1 cm in diameter, tessellate on inner surface, strongly constricted at narrowly ringed throat, the lobes triangular-ovate, 1–1.4 cm by 9–10 mm, with small rugose, papillate area at base; anthers with connective produced, rounded with notch at apex; ovary ± superior, the styles united, with 6 short, radiating arms at apex, the stigmas ovoid, terminal.

Type. Hubei, Ichang, on shady and moist mountain slopes, *Yang & Xueh 74004* (holotype, PTM).

Additional specimens examined. **Zhejiang:** Shou-chang, in forests or in open grass land, *Bot. Res. Exped. 27075* (PE); Mt. Peishan, near Kin-hua, *Migo s.n.* (IBK, PE). **Jiangxi:** Lu-shan, *M. C. Wang 707* (LUS, PE); Wu-gung-shan, in shady, moist thickets, *Jiangxi Exped. 530* (PE). **Hunan:** Nan-yueh, Lung-chi, *L. H. Liu 15744* (PE); Heng-shan, *Anonymous 172* (PE).

Asarum ichangense is widely distributed along the Yangtze River and may extend southward into Fujian, Guangdong, and Guangxi provinces. Its leaves vary considerably in shape, size, and color patterns. The close relationship of *A. ichangense* and *A. chinense* is evidenced by their floral structure—both have small flowers with united styles and terminal stigmas. *Asarum chinense* differs, however, in its long, running rhizomes, its acuminate and essentially elliptic-

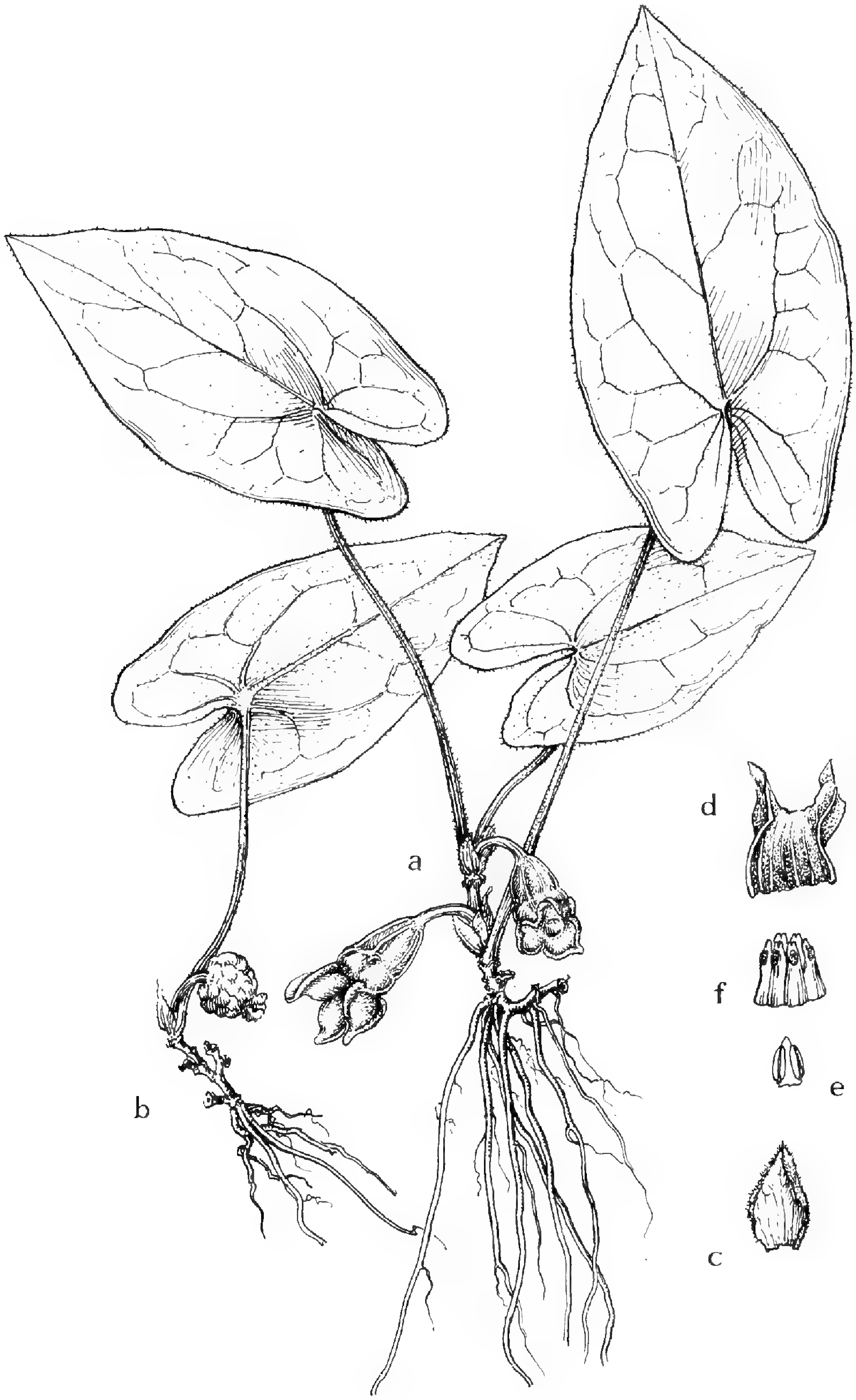

FIGURE 4. **Asarum fukienense:** a, habit of flowering plant, × .65; b, habit of fruiting plant, × .65; c, cataphyll, × 1.3; d, portion of inner surface of perianth tube and reflexed lobe, × 1.3; e, stamen, × 1.3; f, styles, × 2.

ovate leaves, and its perianth tubes with a short neck above the constriction. In *A. ichangense* the rhizomes are perpendicular, short, and thick, the leaves are generally cordate with obtuse or acute apices, and the perianth tubes lack a neck.

14. **Asarum fukienense** C. Y. Cheng & C. S. Yang, sp. nov. FIGURE 4.

Foliis deltoideo-ovatis, foliis subtus et pedunculisque pilis fulvis vestitis, species haec habitu A. wulingense similis, sed lobis perianthii sub anthesis marginibus reflexis, ex medio ad basin pulvinatis, stylis apice stigmatis coronatis interdum apice leviter bilobis lateraliter stigmatosis, differt.

Perennial herbs from short rhizomes with clustered roots. Leaves subcoriaceous, triangular-ovate or narrowly ovate, 4.5–10 by 4–7 cm, acute or shortly pointed at apex, auricular-cordate at base, deep green with occasional white patches above, densely yellowish brown–pubescent below. Flowers purplish green; peduncle 1–2.5 cm long, densely pubescent with soft, yellowish hairs; perianth with the tube cylindrical, 1.5 cm long, 1 cm in diameter, yellowish-pubescent outside, longitudinally ridged on inner surface, lacking constriction or orifice ring at throat, the lobes broadly ovate, 15 by 10 mm, with margins recurved, especially laterally, and with yellowish, semicircular, pulvinate area extending from base to middle; stamens with filament very short, connective pointed; ovary inferior, the styles 6, free, entire (rarely shallowly notched) at apex, the stigmas terminal or subterminal. Capsules ovate-spheroid, 7–17 mm in diameter, often with persistent remains of perianth.

TYPE. Fujian, Wu-i-shan, shady thickets, *M. J. Wang 1929* (holotype, LUS; isotype, PE).

ADDITIONAL SPECIMENS EXAMINED. **Anhui:** Qi-men, in valley in mixed forest, *M. X. Deng 5005* (PE); same locality, at 1500 m, shady moist place, *W. D. Sun 30* (PE); same locality, at 870 m, *J. S. Yueh et al. 5321* (NAS, PE); Wu-i-shan, *M. J. Wang et al. 2418* (LUS, PE). **Fujian:** Shang-hang, *Y. Lin 4150* (PE). **Zhejiang:** Shuei-chang, *Bot. Res. Exped. 25738, 25903* (PE).

Asarum fukienense is characterized by its yellowish brown pubescence and its nonconstricted perianth tubes with the lobes strongly recurved laterally. In overall appearance, *A. fukienense* is similar to *A. wulingense* from Guangxi Province, but the latter differs considerably in having constricted perianth tubes with spreading, nonrecurved perianth lobes, distinct styles with bifid apices, and lateral stigmas.

Asarum ser. **Bicorne** Araki, Acta Phytotax. Geobot. **6:** 127. 1937.

Perianth with the tube 1–2 cm long (rarely longer), longitudinally ridged or tessellate internally, constricted at throat, orifice evident and often having laminate ring, the lobes having papillate or pulvinate area at base. TYPE SPECIES: *Asarum asaroides* (Morren & Dcne.) Makino.

Fourteen species and one variety in China.

FIGURE 5. **Asarum chingchengense:** a, habit of flowering plant, × .6; b, cataphyll, × 1.2; c, portion of inner surface of perianth tube and lobe, × 1.5; d, flower with perianth removed, showing androecium and gynoecium, × 2.4; e, stamens, × 1.2; f, bifid style tips and lateral stigmas, × 1.2.

15. **Asarum chingchengense** C. Y. Cheng & C. S. Yang, sp. nov. FIGURE 5.

Tubis perianthii leviter constrictis, ovariis subsuperioribus haec nova species habitu A. taitinensi similis, sed tubis perianthii cupularis non profundis ad orem leviter constrictis ad maximam aperturam, foliis et petiolis pedunculique glabris, differt.

Perennial herbs from long, horizontal rhizomes, internodes ca. 1.5 cm long with ± thick and fleshy roots clustered at nodes. Leaves with petiole 6–18 cm long, the cataphylls at its base triangular-ovate, 2 by 1.5 cm, ciliate; blade ovate-cordate, long-ovate, or nearly hastate, 6–10 by 5–9 cm, acute at apex, deeply auriculate or subcordate at base, green, usually with white blotches and sparingly pubescent above, glabrous beneath. Flowers purplish green; peduncle ca. 2 cm long; perianth having the tube cupular or hemispherical, ca. 1.4 cm long, 2 cm in diameter, slightly constricted at throat, orifice large with ring very narrow and inconspicuous, inner surface tessellate, the lobes broad-ovate, ca. 2 by 2.5, with semicircular, rugose, papillate area at base; stamens with filament very short, connective rounded; ovary ± superior, the styles 6, free, forked or notched at apex, the stigmas ovoid, lateral.

TYPE. Sichuan, Guan-xien, moist slopes in thickets or partial shade, *C. Y. Cheng & C. S. Yang 63001* (holotype, PEM).

ADDITIONAL SPECIMENS EXAMINED. **Sichuan:** Ching-cheng-shan, *F. T. Wang 20386* (PE); Chung-qing, Jin-yun-shan, *C. Y. Cheng & C. S. Yang s.n.* (PEM, PTM). **Guizhou:** Meitan, *J. M. Chen 207* (PE); Chishuei, *X. L. Chen 005* (GIM).

Asarum chingchengense is closely related to *A. taitonense* Hayata from Taiwan, which differs from the Sichuan plant in having deeper perianth tubes with a narrower throat, and pubescent lower leaf surfaces, petioles, and peduncles.

16. **Asarum forbesii** Maxim. Bull. Acad. Sci. St.-Pétersb. **31:** 92. 1887. TYPE: N. Zhejiang, *Forbes 2056* (photo PE).

DISTRIBUTION. Henan, Anhui, Jiangsu, Jiangxi, Hubei, Hunan, and Sichuan. Fairly common in thickets and forests; 200–800 m alt.

17. **Asarum taitonense** Hayata, Ic. Pl. Formosa. **5:** 148. 1915; Liu & Lai *in* Li, Fl. Taiwan **2:** 581. 1976. TYPE: Taiwan, Mt. Taiton, *Faurie s.n.* (photo of fragment PE).

Heterotropa taitonensis (Hayata) Maekawa ex Nemoto, Fl. Jap. Suppl. 165. 1936; Jour. Jap. Bot. **53:** 299. 1978.

DISTRIBUTION. Endemic to Taiwan. In forests and thickets; low to medium altitudes.

18. **Asarum infrapurpureum** Hayata, Ic. Pl. Formosa. 146. 1915; Liu & Lai *in* Li, Fl. Taiwan **2:** 579. 1976. TYPE: Taiwan, *Sasaki s.n.* (n.v.).

DISTRIBUTION. Endemic to northern Taiwan. In thickets and wet places.

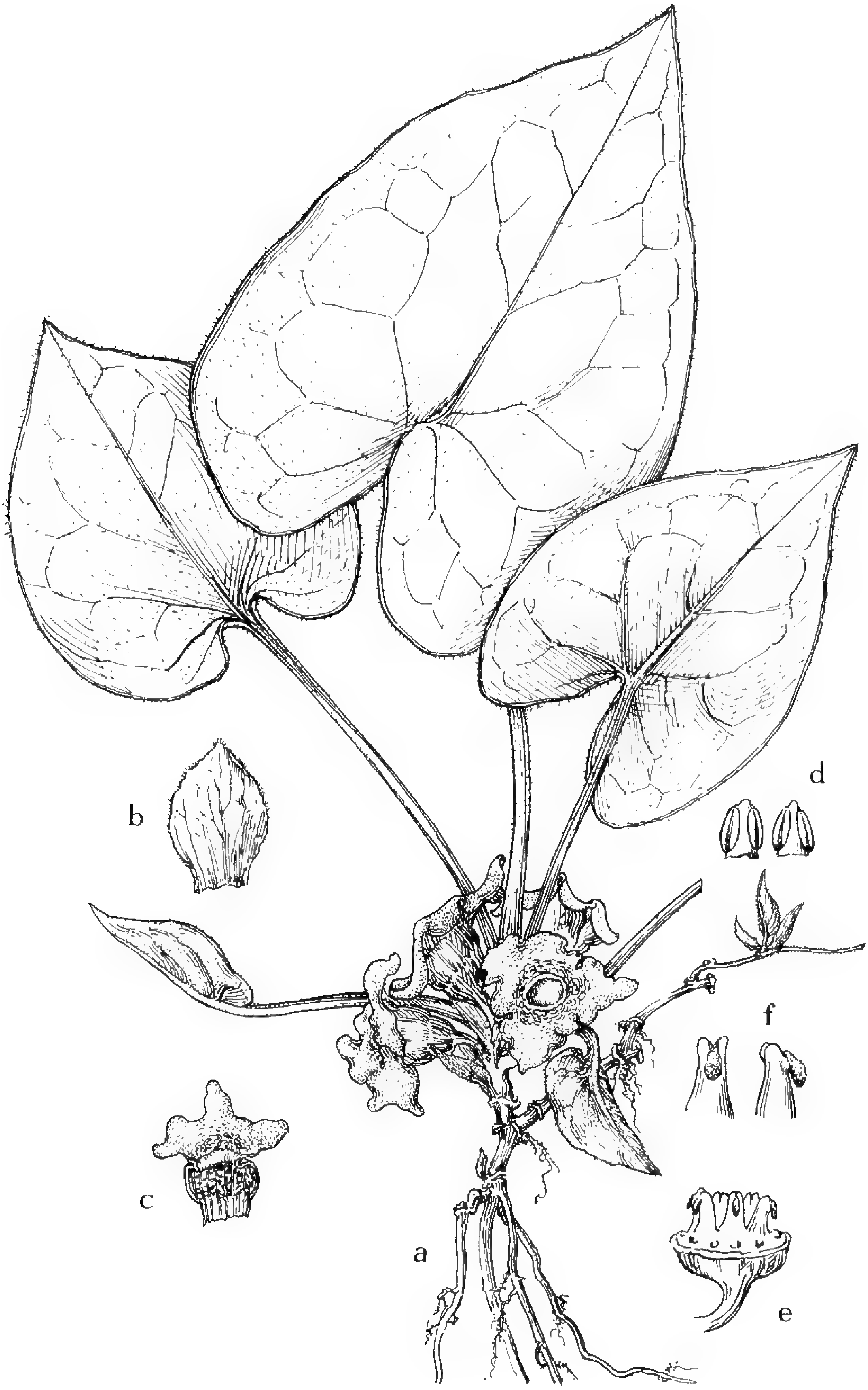

FIGURE 6. **Asarum crispulatum:** a, habit of flowering plant, × .65; b, cataphyll, × 1.3; c, longitudinal section through perianth, × .65; d, stamens, × 1.3; e, gynoecium, × 1.3; f, styles, × 1.3.

19. **Asarum macranthum** Hooker f. Curtis's Bot. Mag. **116:** *t. 7022.* 1888; Liu & Lai *in* Li, Fl. Taiwan **2:** 579. 1976; Maekawa, Jour. Jap. Bot. **53:** 296. 1978. TYPE: Taiwan, Kelung, *Ford s.n.* (K, n.v.).

DISTRIBUTION. Endemic to Taiwan. Forested habitats; low to medium altitudes.

Although J. D. Hooker did not designate a type for *Asarum macranthum,* he did indicate the sources of the dried specimens and the living plants utilized in drawing up his description. The material at Kew collected by Ford should be studied if a lectotype is to be selected.

20. **Asarum crispulatum** C. Y. Cheng & C. S. Yang, sp. nov. FIGURE 6.

Affinis A. macranthi sed lobis perianthii modice undulatis, staminibus triangularibus, foliis subtus viridibus non rubris nervis et petiolis non-maculatis, differt.

Perennial herbs from short rhizomes with clustered roots. Leaves with petiole 6–15 cm long, pubescent with short, soft hairs, the cataphylls at its base ovate, ca. 2 by 1.3 cm, ciliate; blade ovate-cordate or narrowly ovate, 5–9 by 2–2.5 cm, acute or short-acuminate at apex, cordate or auricular-cordate at base, deep green with occasional whitish patches and scattered hairs above, light green and glabrous beneath. Flowers purplish green, ca. 3–5 cm across; peduncle ca. 1 cm long; perianth having the tube urceolate, ca. 1.5 cm long, 1.2–2 cm in diameter, orifice small with ring ca. 1.5 mm broad, inner surface tessellate, the lobes ovate, 1.8–2.2 by 2–2.6 cm, margins ± undulate; stamens triangular, the filament short, broadened at base, the connective acute or obtuse at apex; ovary half inferior, the styles 6, bifid at apex, the stigmas oblong-ovoid, inserted in notch and hanging free, free end slightly hooked.

TYPE. Sichuan, Nan-chuan, in moist habitat, *Yang & Li 72004* (holotype, PTM).

ADDITIONAL SPECIMENS EXAMINED. **Sichuan:** without further locality, *Yang 78-lan-001* (OTS). **Cultivated:** hort. Beijing Medical College, *Cheng 7808* (PEM).

Asarum crispulatum is allied to *A. macranthum,* which differs in having blotched or spotted petioles, strongly undulate perianth lobes, linear-oblong stamens with notched connectives, and strongly hooked stigmas. The specific epithet of the new species, *crispulatum,* refers to its undulate perianth lobes.

21. **Asarum delavayi** Franchet, Bull. Mus. Hist. Nat. Paris **1:** 66. 1895; Jour. Bot. Morot **12:** 304. 1898. SYNTYPES: Yunnan, Long-ki, *Delavay 5105* (P, photo PE), *Delavay 5205* (P, n.v.).

Heterotropa splendens Maekawa, Jour. Jap. Bot. **57:** 261. *pl. 14.* 1982.

DISTRIBUTION. Sichuan and northern Yunnan. Shady, moist slopes of forests and thickets, usually of southern exposure; 800–1600 m alt.

The leaves of *Asarum delavayi* are variable in both shape and coloration. They are generally large (9–18 by 6–14 cm), with the upper surface green and the lower surface light green. Some leaves are occasionally found with white blotches above or reddish purple coloration below, and other leaves combine these color variations.

22. **Asarum porphyronotum** C. Y. Cheng & C. S. Yang, sp. nov. FIGURE 7.

Similis A. delavayi, sed differt foliis subtus semper purpureis, floribus pluribus minoribus urceolatis circa 2.5 cm longis et 2–2.5 cm in diametro, tubis perianthii brevioribus ovaliformibus circum oreum intus angustatis annulis instructis, connectivis antherarum apice breviori-pyramidalibus.

Perennial herbs from short rhizomes. Leaves with petiole purplish or purplish brown, the cataphylls at its base usually 2, broadly ovate, lower one larger, ciliate; blade elliptic-oblong to broadly ovate (rarely subhastate), 5–15 by 6–13 cm, acute or obtuse at apex, auriculate to cordate at base, margin ciliate, dull green and white-blotched above, purplish red below. Flowers purple, 2–2.5 cm in diameter; peduncle ca. 1 cm long; perianth having the tube urceolate, ca. 12 mm long, 11–14 mm in diameter, constricted and with narrow orifice ring, tessellate internally, the lobes broadly triangular-ovate, ca. 8 by 11 mm, densely papillate in triangular pattern at base; stamens with filament very short, connective acute; ovary ± superior, the styles 6, bifid at apex, the stigmas ovoid, lateral.

TYPE. Sichuan, without precise locality, *Cheng 7501* (holotype, PEM; isotype, PTM).

ADDITIONAL SPECIMENS EXAMINED. **Cultivated:** hort. Beijing Medical College, *Cheng 7601, 7607, 7816, 7944* (PEM).

Related to *Asarum delavayi* Franchet, *A. porphyronotum* is characterized by its urceolate perianth tubes, its very narrow orifice ring, its shortly acute anther connectives, and its leaves with persistent white patches above and purplish red coloration below. *Asarum delavayi,* by contrast, has larger flowers (3–4 cm long and 4–6 cm in diameter), with the perianth tubes usually constricted near the apex and then dilated, forming a collar. The specific name of the new species refers to the purplish red undersurfaces of the leaves.

22a. **Asarum porphyronotum** var. **atrovirens** C. Y. Cheng & C. S. Yang, var. nov. FIGURE 8.

A varietate typica differt foliis angustioribus paribus supra atroviridibus nunquam praeditis albo-maculatis, connectivis antherarum apice haud productis.

TYPE. Sichuan, without precise locality, *Cheng 7562* (holotype, PEM; isotype, PTM).

This new variety is readily separated from *Asarum porphyronotum* var. *porphyronotum* in having lustrous, deep green leaves that are never dull green or white-blotched above or purplish red below. In addition, the flowers are often smaller, and the stamen connectives are rounded. The epithet, *atrovirens,* refers to the color of the leaves.

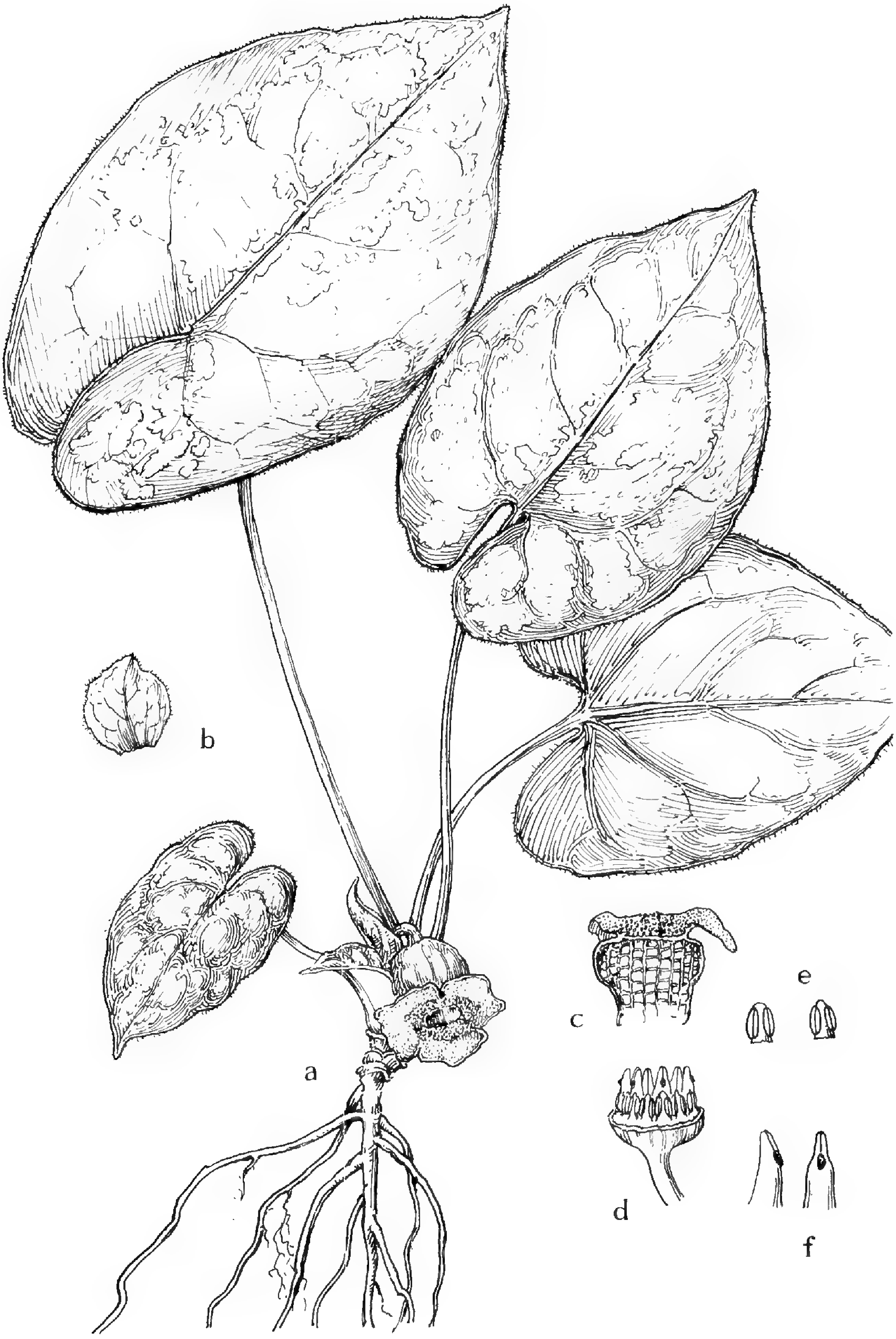

FIGURE 7. **Asarum porphyronotum:** a, habit of flowering plant, × .65; b, cataphyll, × .65; c, longitudinal section through perianth, showing inner surface, × 1.3; d, flower with perianth removed, showing androecium and gynoecium, × 1.3; e, stamens, × 1.3; f, styles and stigmas, × 1.3.

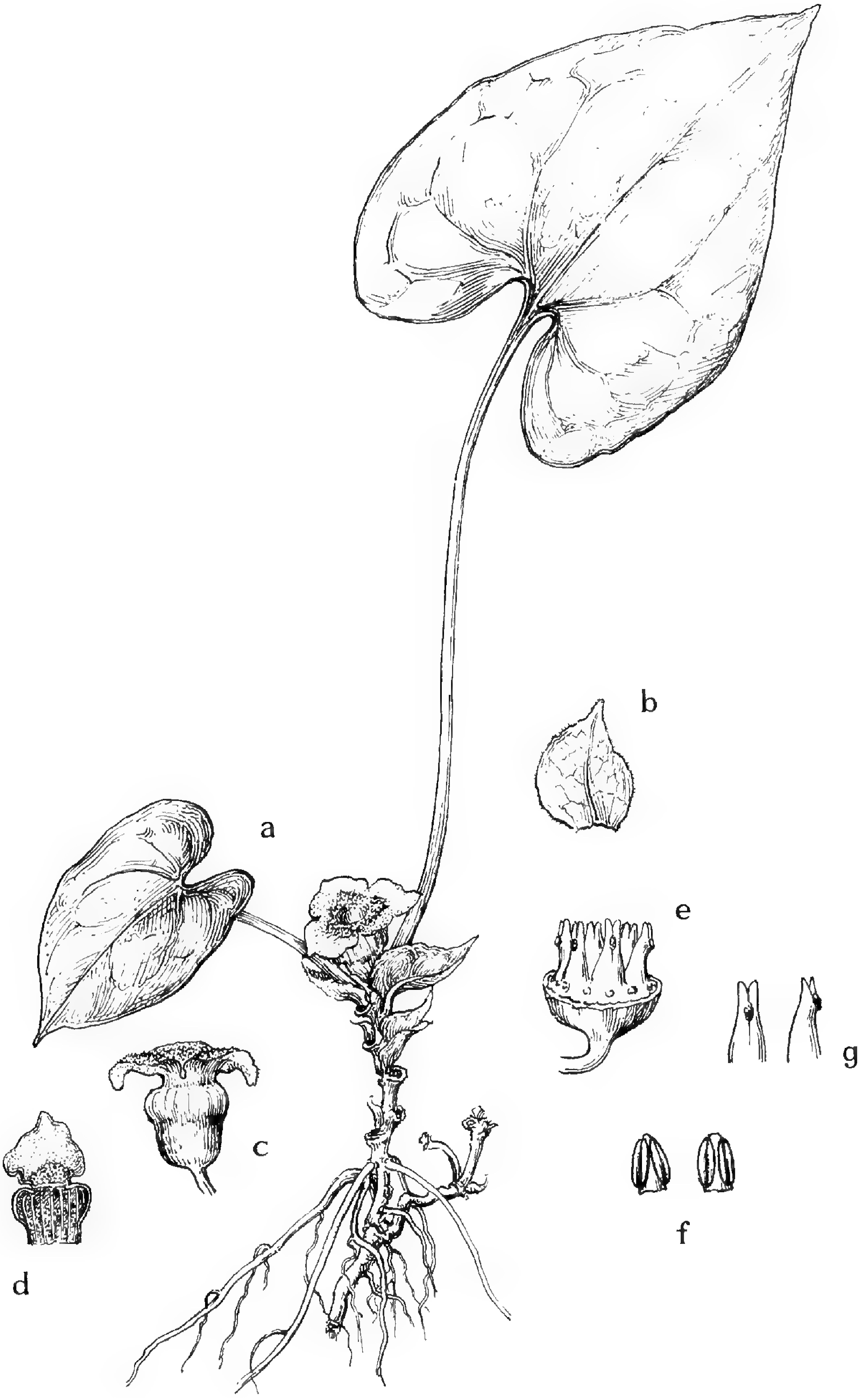

FIGURE 8. **Asarum porphyronotum** var. **atrovirens:** a, habit of flowering plant, × .7; b, cataphyll, × 1.4; c, flower, lateral view, × 1; d, portion of perianth, showing inner surface of tube and lobe, × 1; e, flower with perianth and androecium removed, showing gynoecium, × 1.75; f, stamens, × 1.4; g, styles and stigmas, × 1.4.

23. **Asarum inflatum** C. Y. Cheng & C. S. Yang, sp. nov. FIGURE 9.

Planta tubo perianthii supra medium extus annulo crasso cincto A. maximo affinis, sed tubis perianthii valde constrictis, annulo crassiore altioreque intus longitudinaliter crassius plicato, lobis perianthii longe ovatis basi papillato-rugosis haud pulvinatis, differt.

Perennial herbs with short rhizomes and numerous ± fleshy roots. Leaves with petiole 7–10 cm long, the cataphylls at its base ovate, ca. 1.5 cm long, densely ciliate; blade ovate, triangular-ovate, or nearly hastate, 4–11 by 5–11 cm, acute at apex, auriculate at base with divaricate lobes, shortly pubescent on veins above, glabrous beneath. Flowers dull purple; peduncle ca. 1 cm long; perianth having the tube lantern shaped, with the lower portion broadly cylindrical, ca. 1 cm long, 1.5 cm in diameter, densely striate, and with the upper portion abruptly swollen into broad, hollow disc ca. 9 mm high, 2 cm in diameter, longitudinally ridged externally, rugosely ribbed internally, constricted at apex into narrow orifice with broad, flat ring, the lobes ovate, to 3.5 by ca. 2.5 cm, with triangular, rugose, papillate area at base continuing to orifice; stamens with filament very short and anther connective obtuse; ovary half inferior, the styles 6, apices bifid and hornlike, stigmas lateral below notches.

TYPE. Sichuan, Cang-xi, moist places in ravine and rock fissures, at 1000 to 1400 meters, *Anonymous 72N-576* (holotype, SIT).

ADDITIONAL SPECIMEN EXAMINED. **Sichuan:** Wang-cang, *Sichuan Econ. Exped. 4747* (SIT).

The flowers of *Asarum inflatum,* like those of *A. maximum,* are relatively large and prominently swollen. However, in *A. inflatum* the swollen portion is near the top of the perianth tube and is broad with vertical ridges. In *A. maximum,* by contrast, the swollen area occurs at the center of the tube and is girdlelike, and the prominent ridges are lacking. The perianth lobes of *A. inflatum* are beset with rough papillae, while those of *A. maximum* have only a pulvinate region. The epithet *inflatum* has been applied to this new species because of its swollen perianth tubes.

24. **Asarum maximum** Hemsley, Gard. Chron. III. **7:** 422. 1890; Jour. Linn. Soc. Bot. **26:** 359. 1891; J. D. Hooker, Curtis's Bot. Mag. **122:** *t. 7456.* 1896. TYPE: Hubei, Ichang, *Henry 3669* (K, n.v., photo PE).

DISTRIBUTION. Hubei and eastern Sichuan. On cliff faces and in litter on forest floors; 600–800 m alt.

25. **Asarum insigne** Diels, Notizbl. Bot. Gart. Berlin-Dahlem **10:** 855. 1930. TYPE: Guangxi, Da-yao-shan, *C. Wang 39031* (isotype, SYS).

Asarum longepedunculatum Schmidt, Sunyatsenia **1:** 121. *pl. 30.* 1933. TYPE: Guangdong, Ying-de, *S. P. Ko 50476* (isotype, SYS).

Asarum gracilipes C. S. Yang, Acta Phytotax. Sinica **13**(2): 19. *pl. 4, figs. 3–8.* 1975. TYPE: Guangxi, Xing-an, *C. F. Liang 34161* (holotype, IBK).

DISTRIBUTION. Guangdong and Guangxi. Moist, shady forests; frequent at ca. 500 m alt.

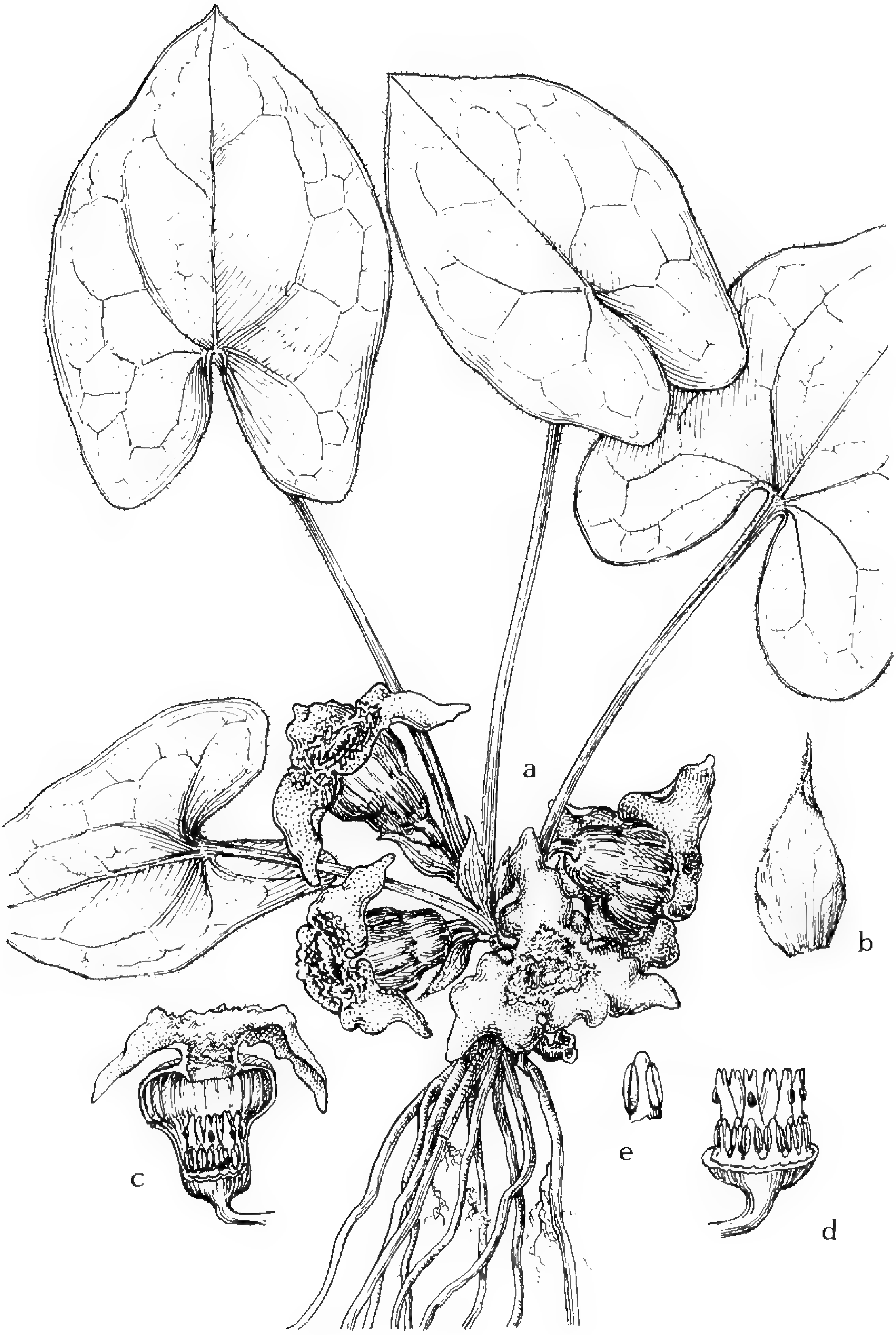

FIGURE 9. **Asarum inflatum:** a, habit of flowering plant, × .62; b, cataphyll, × 1.25; c, longitudinal section through flower, × .62; d, flower with perianth removed, showing androecium and gynoecium, × 1.25; e, stamen, × 1.25.

When he described *Asarum longepedunculatum*, Schmidt stated that it differed from *A. insigne* in having longer (to 9 cm) peduncles and obtuse anther connectives. As more material has become available, however, it has become evident that these are both variable characters and that *A. longepedunculatum* cannot be maintained. Likewise, *A. gracilipes* is merely a slender form of *A. insigne*, and Yang's name is placed in the synonymy of *A. insigne*.

26. **Asarum nanchuanense** C. S. Yang & J. L. Wu,[3] sp. nov. FIGURE 10.

Habitu species nova A. maximo similis, sed tubo perianthii extus annulatis crassis nullis, lobis perianthii basi minime pulvinatis non papillato-rugosis, foliis subtus purpureis, differt.

Perennial herbs from short rhizomes and ± fleshy roots. Leaves with petiole 2.5–7.5 cm long, the cataphylls at its base broadly ovate, 2 by 1.8 cm, ciliate; blade cordate, 5–7 by 6–8.5 cm, the lobes at base 2–2.5 cm long, the upper surface deep green with white blotches, shortly pubescent along lateral veins, the lower surface reddish purple. Flowers 3–4 cm across; peduncle ca. 1.5 cm long; perianth with the tube cylindrical, 2–2.5 cm long, ca. 2 cm in diameter, slightly constricted, with large, naked orifice, ring inconspicuous, internal surface usually with 10 longitudinal ridges, the lobes broadly ovate, ca. 1.5 cm long, having small pulvinate areas ca. 2 mm in diameter at base; stamens with filament very short, anther connective produced into acute apex; ovary inferior, the styles 6, apically notched, the stigmas outside notches.

TYPE. Sichuan, Nan-chuan, Cha-sha, in rock crevices in thickets, *Z. L. Yang 37* (holotype, PTM).

ADDITIONAL SPECIMENS EXAMINED. **Sichuan:** Nan-chuan, *C. S. Yang 72004* (PEM, PTM).

Allied to *Asarum maximum* of Hubei Province, *A. nanchuanense* differs from that species in having gradually dilated perianth tubes that lack a girdlelike dilated zone, and perianth lobes with only a small pulvinate area near the base. Moreover, there is no white collar, and papillae are absent around the orifice. The specific name is derived from the type locality in Sichuan Province.

27. **Asarum sagittarioides** C. F. Liang, Acta Phytotax. Sinica **13**(2): 23. *pl. 5, figs. 7–11.* 1975. TYPE: Guangxi, Jin-xiu, *K. Y. Li 40958* (holotype, IBK).

DISTRIBUTION. Endemic to Guangxi Province. On slopes and near streams, usually under thickets; 900–1200 m alt.

28. **Asarum longerhizomatosum** C. F. Liang & C. S. Yang, Acta Phytotax. Sinica **13**(2): 21. *pl. 1, fig. 2; pl. 2, figs. 4–10.* 1975. TYPE: Guangxi, Daming-shan, *C. L. Chang 001* (isotype, PTM).

DISTRIBUTION. Endemic to Guangxi. Open thickets or sunny, rocky areas.

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[3] J. L. Wu, formerly of the Beijing Chinese Traditional Medicinal College, Beijing, is a student of the Aristolochiaceae who is collaborating with Professor Yang; he is now at the Sichuan Chinese Traditional Medicinal School, Omei.

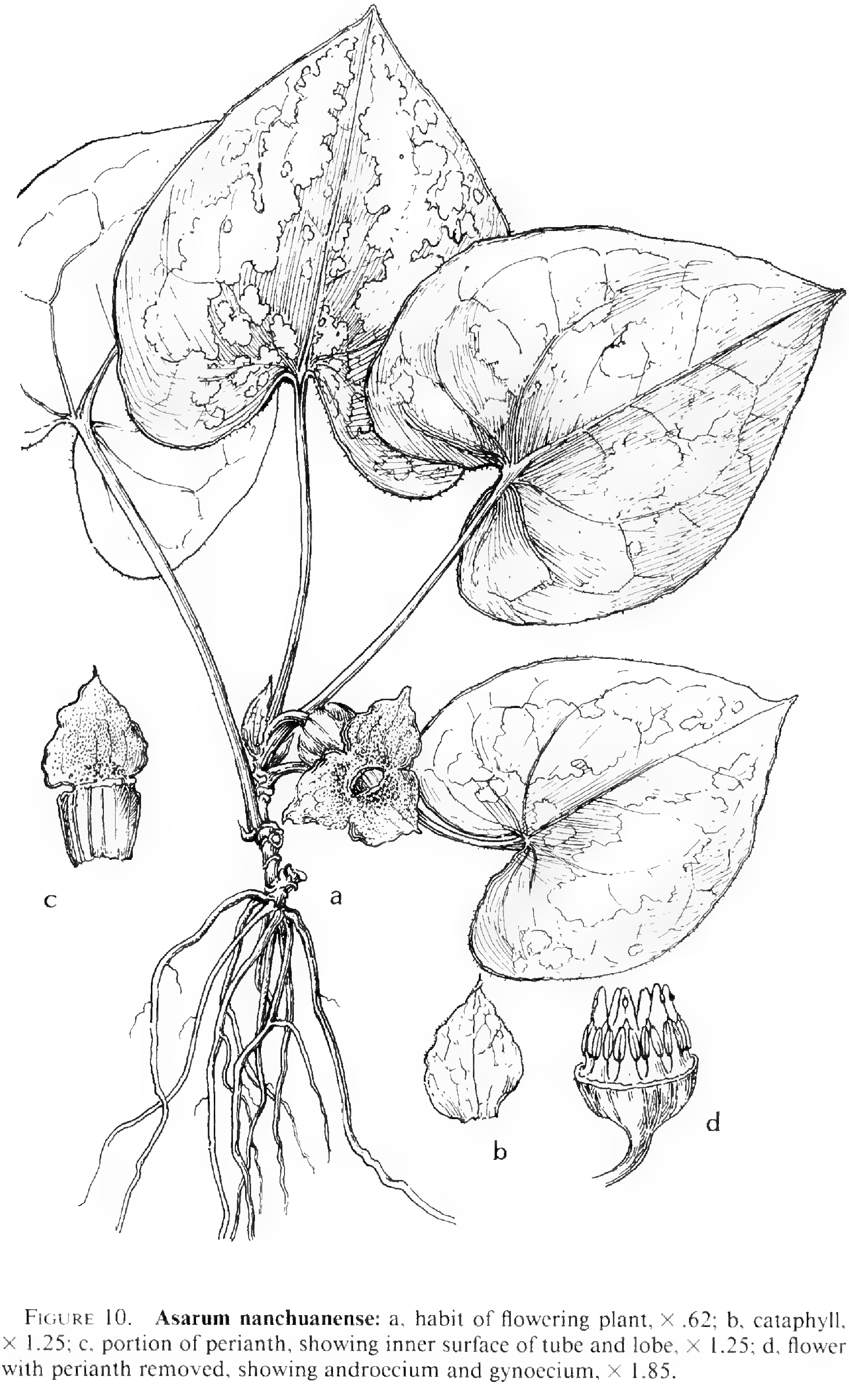

FIGURE 10. **Asarum nanchuanense:** a, habit of flowering plant, × .62; b, cataphyll, × 1.25; c, portion of perianth, showing inner surface of tube and lobe, × 1.25; d, flower with perianth removed, showing androecium and gynoecium, × 1.85.

29. **Asarum wulingense** C. F. Liang, Acta Phytotax. Sinica **13**(2): 22. *pl. 5, figs. 1–6.* 1975. TYPE: Guangxi, Lung-sheng, *S. L. Yu & H. F. Qin 700702* (holotype, IBK).

DISTRIBUTION. Hunan, Guangdong, and Guangxi. 800–1000 m alt.

This species is one of the few in *Asarum* that has an indumentum of soft, yellowish brown hairs.

Asarum sect. **Longiflora** C. Y. Cheng & C. S. Yang, sect. nov.

Tubis perianthii longis et infundibuliformibus non constrictis nonnunquam leviter constrictis, sine annulo ad orem, papillis remote dispositis e medio loborum ad imum tubo in seriebus verticalibus. TYPE SPECIES: *Asarum magnificum* Tsiang ex Cheng & Yang (Hunan).

Two species and one variety in China.

30. **Asarum magnificum** Tsiang ex C. Y. Cheng & C. S. Yang, sp. nov. FIGURE 11.

Asarum magnificum Tsiang, Fl. Hupehensis **1**: 208. *fig. 278.* 1976. Description in Chinese, lacking a Latin diagnosis.

Heterotropa magnifica (Tsiang) Maekawa, Jour. Jap. Bot. **57**: 262. 1982. An invalid new combination based on *Asarum magnificum* Tsiang, *ibid.*

Planta floribus maximis, tubis perianthii longissimis intus sparsim longitudinaliter papillato-rugosis a A. petelotio similis, sed tubis perianthii erectis ad orem haud constrictis circum orem annulatis non instructis, foliis triangulari-ovatis vel oblongo-ovatis apice acutis vel breve acuminatis supra ad costam albo-maculatis, rhizomatis brevioribus, differt.

Perennial herbs from short rhizomes with clustered, ± fleshy roots. Leaves with petiole 6–16 cm long, the cataphylls at its base 3 or 4, ovate, ca. 1.5 cm long, densely ciliate; blade subcoriaceous, triangular- or oblong-ovate, 6–13 by 5–12 cm, acute or acuminate at apex, auriculate at base, white-blotched along midvein above (midvein often covered by short hairs), glabrous below. Flowers purplish green, large, 4–5 cm across, peduncle ca. 1.5 cm long; perianth with the tube funnelform, 3–5 cm long, 1.5 cm in diameter, not constricted (hence no definite orifice), internal surface having large papillae in vertical rows (toward base these often replaced by longitudinal ridges), the lobes triangular-ovate, ca. 3 by 2–2.5 cm, having purplish crescent toward middle and triangular, papillate area beneath continuous with papillae of tube; anthers with connective acute; ovary inferior, the styles 6, free, bifid at apex, the stigmas lateral.

TYPE. Hunan, Qi-yang, in shade, *Y. Tsiang & S. C. Chen 859* (holotype, IBSC).

ADDITIONAL SPECIMENS EXAMINED. **Jiangxi:** Da-mao-shan, beside stream, in shade, 700 m, *W. D. Yang 24* (LUS). **Zhejiang:** Chun-an, *Bot. Res. Exped. 27513* (HIM).

In addition to its distribution in Hunan, Jiangxi, and Zhejiang provinces, *Asarum magnificum* is also known to us to occur in Hubei and Guangdong

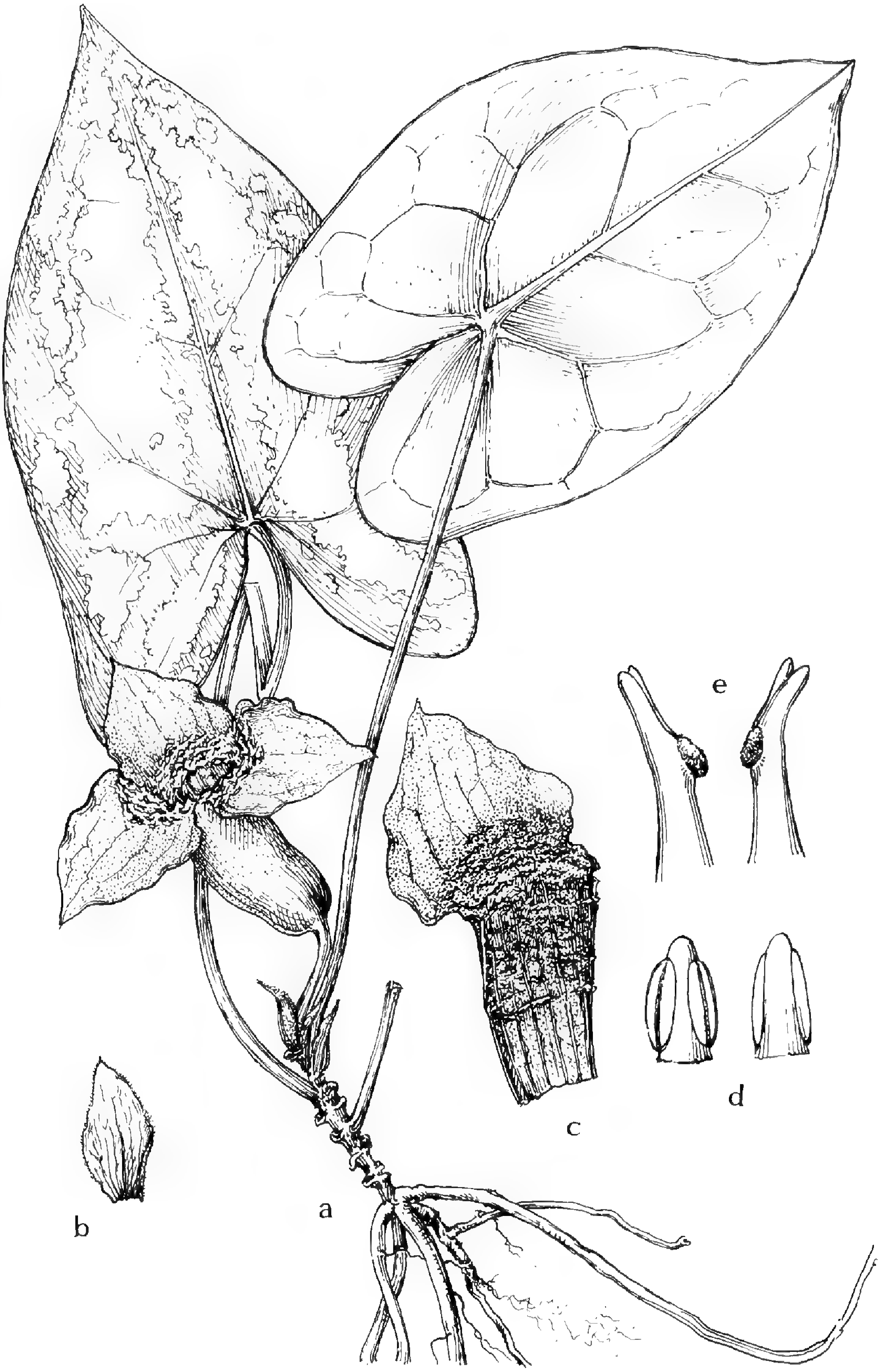

FIGURE 11. **Asarum magnificum:** a, habit of flowering plant, × .65; b, cataphyll, × .65; c, portion of perianth, showing inner surface of tube and lobe, × 1; d, stamens, × 2.6; e, styles and lateral stigmas, × 2.6.

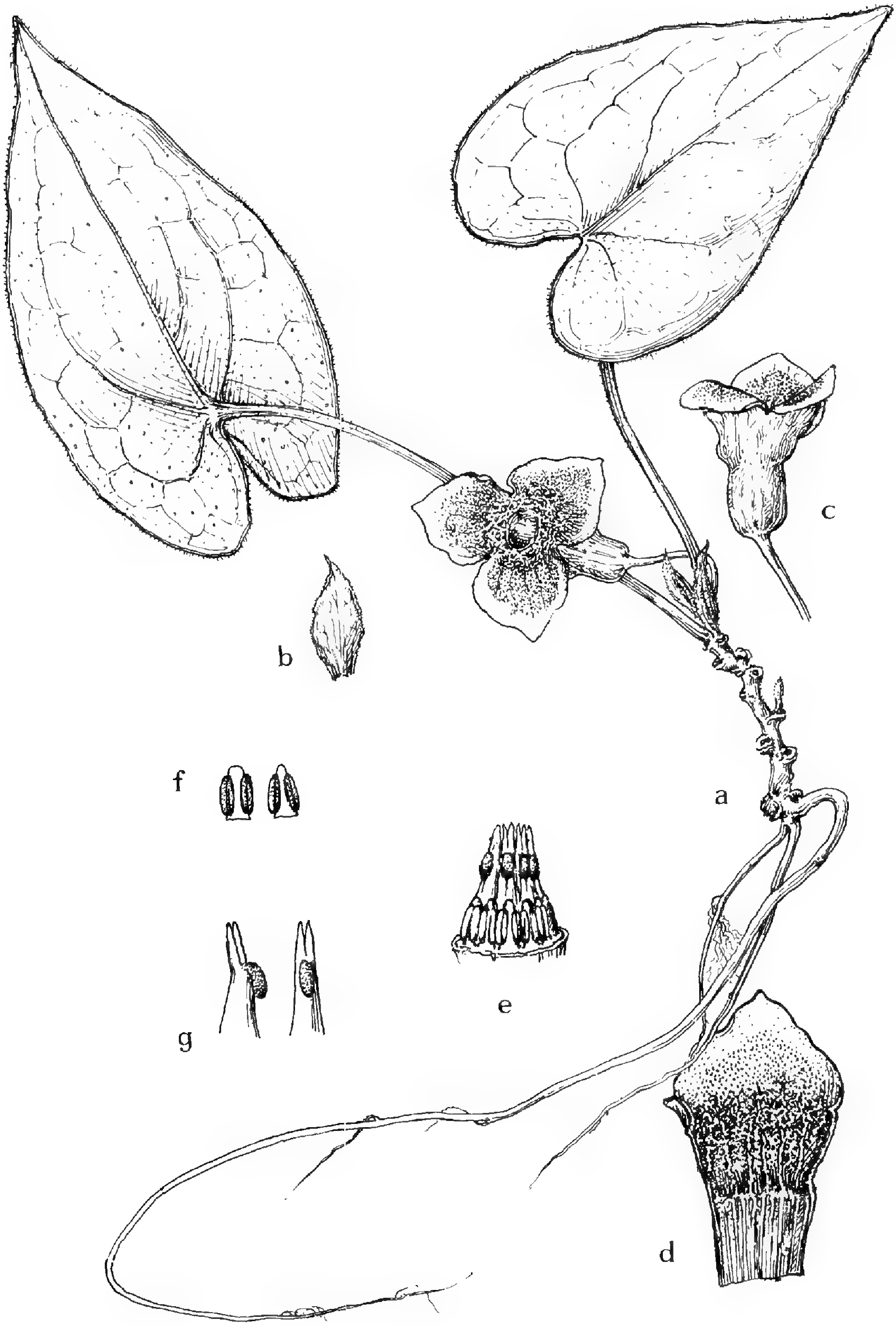

FIGURE 12. **Asarum magnificum** var. **dinghuense:** a, habit of flowering plant, × .62; b, cataphyll, × .62; c, flower, lateral view, × .62; d, portion of perianth, showing inner surface of tube and lobe, × 1.25; e, flower with perianth removed, showing androecium and gynoecium, × 1.25; f, stamens, × 1.25; g, styles and stigmas, × 1.25.

provinces and probably also grows in Shaanxi. *Asarum magnificum* was initially identified and named in the herbarium of Guangdong College of Agriculture and Forestry by Professor Ying Tsiang, but it was never published. It is closely related to *A. petelotii*, from Yunnan southward into Indochina, and both species are characterized by their large flowers with unconstricted perianth tubes that lack an orifice ring but have large papillae on the inner surface. *Asarum magnificum*, however, is distinguished by its straight, symmetrical perianth tubes, its triangular- or oblong-ovate leaves with acute apices and white-blotched upper surfaces, and its very short, nearly perpendicular rhizomes.

30a. **Asarum magnificum** var. **dinghuense** C. Y. Cheng & C. S. Yang, var. nov. FIGURE 12.

A typo tubis perianthii brevioribus circum 1 cm longis et 8 mm in diametro et supra medium ad 1 cm in diametro dilatis, intus tenuiter et parce papillosis, foliis saepe ovato-oblongis supra non albo-maculatis parce breviter hirtis subtus interdum oleosipunctatis, differt.

TYPE. Guangdong, Chao-qing, Ding-hu-shan, alt. 300–700 m, in damp, shady thickets, *G. Q. Ding et al. 1039* (IBSC).

ADDITIONAL SPECIMENS EXAMINED. **Guangdong:** Ding-hu-shan, *L. Teng 11066* (IBSC); Xin-i, *C. Wang 37999* (IBSC).

Asarum magnificum var. *dinghuense* differs from var. *magnificum* in having smaller flowers with fewer papillae on the perianth lobes, and leaves green throughout, sometimes with punctate lower surfaces.

31. **Asarum petelotii** Schmidt, Notizbl. Bot. Gard. Berlin-Dahlem **11:** 100. 1931. TYPE: Vietnam, Tonkin, *Pételot 3891* (B, n.v.).

DISTRIBUTION. Southeastern Yunnan; also Vietnam. In moist, forested areas; 1100–1700 m alt.

Previously unrecorded for China, this species has large flowers with the perianth tubes slightly asymmetric due to a bend to one side.

ACKNOWLEDGMENTS

Deep appreciation is extended to P. S. Ashton and P. F. Stevens for their encouragement in this work. We also wish to extend our sincere thanks to S. A. Spongberg for his help in reading the manuscript and in making many valuable suggestions and criticisms. Thanks are also due Wei-cheng Zung, Professor Emeritus, College of Forestry, Beijing, for his illustrations of the new species.

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MAEKAWA, F. 1932. Alabastra diversa I. Bot. Mag. Tokyo **46:** 561–586.

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C. Y. C.
DEPARTMENT OF PHARMACEUTICAL SCIENCE
BEIJING MEDICAL COLLEGE
BEIJING
PEOPLE'S REPUBLIC OF CHINA

C. S. Y.
BEIJING CHINESE TRADITIONAL
MEDICINAL COLLEGE
BEIJING
PEOPLE'S REPUBLIC OF CHINA

ANATOMY OF THE PALM RHAPIS EXCELSA, IX. XYLEM STRUCTURE OF THE LEAF INSERTION

MARTIN H. ZIMMERMANN AND JOHN S. SPERRY

STEMS OF PERENNIAL PLANTS, particularly trees, represent a considerable investment in biomass. Trees can survive even under the most adverse conditions, but only if the hydraulic integrity of the stem is preserved. A very important and vulnerable part of the stem is the xylem. As water is pulled into the top of the tree, a period of excessive drought can drop xylem pressures to such low negative values that water columns break (cavitation). The tracheary elements in which this happens are permanently lost as functional parts unless positive pressures refill them within a very short time (perhaps hours?). We have recently found that the xylem of trees is constructed in such a way that under conditions of severe drought the hydraulic integrity of the stem is favored at the expense of leaves or even branches (Zimmermann, 1978). The principle of this construction works as follows: the resistance to flow in the tracheary elements is much lower in the stem than in the peripheral parts (leaves, twigs, branches). Under transpirational conditions pressures therefore drop to much lower levels in the peripheral organs than in the stem. If pressures drop to disastrously low levels, water columns break first in leaves, later in lateral axes, and last in the stem. This quantitatively adjusted xylem construction is referred to as the hydraulic architecture of the plant (Zimmermann, 1978).

Although hydraulic architecture appears to be important as a mechanism for controlling cavitation in dicotyledonous and coniferous trees, such trees at least have the advantage of being able to renew lost xylem by cambial activity. In contrast, palms and other arborescent monocotyledons that have no secondary growth are entirely dependent on primary vascular stem tissue throughout their entire life. Prevention of permanent embolism in the stem is therefore of paramount importance for the survival of palms. From our earlier investigations of palm-stem anatomy (Zimmermann & Tomlinson, 1965), we know that the xylem that connects stem and leaves consists of very narrow tracheary elements. This indicates, at least qualitatively, that the leaf insertion represents a hydraulic bottleneck. In this paper qualitative and quantitative anatomical analysis of the stem-to-leaf vascular connection will provide the basis for discussing the hydraulic architecture of *Rhapis* and how it may work to preserve the functionality of the stem. According to our hypothesis, the hydraulic bottleneck in the leaf insertion is absolutely essential for the survival of palms. In this series of papers we have used *Rhapis* as a model for all palms—a reasonable assumption supported by substantial comparative evidence (Zimmermann & Tomlinson, 1974).

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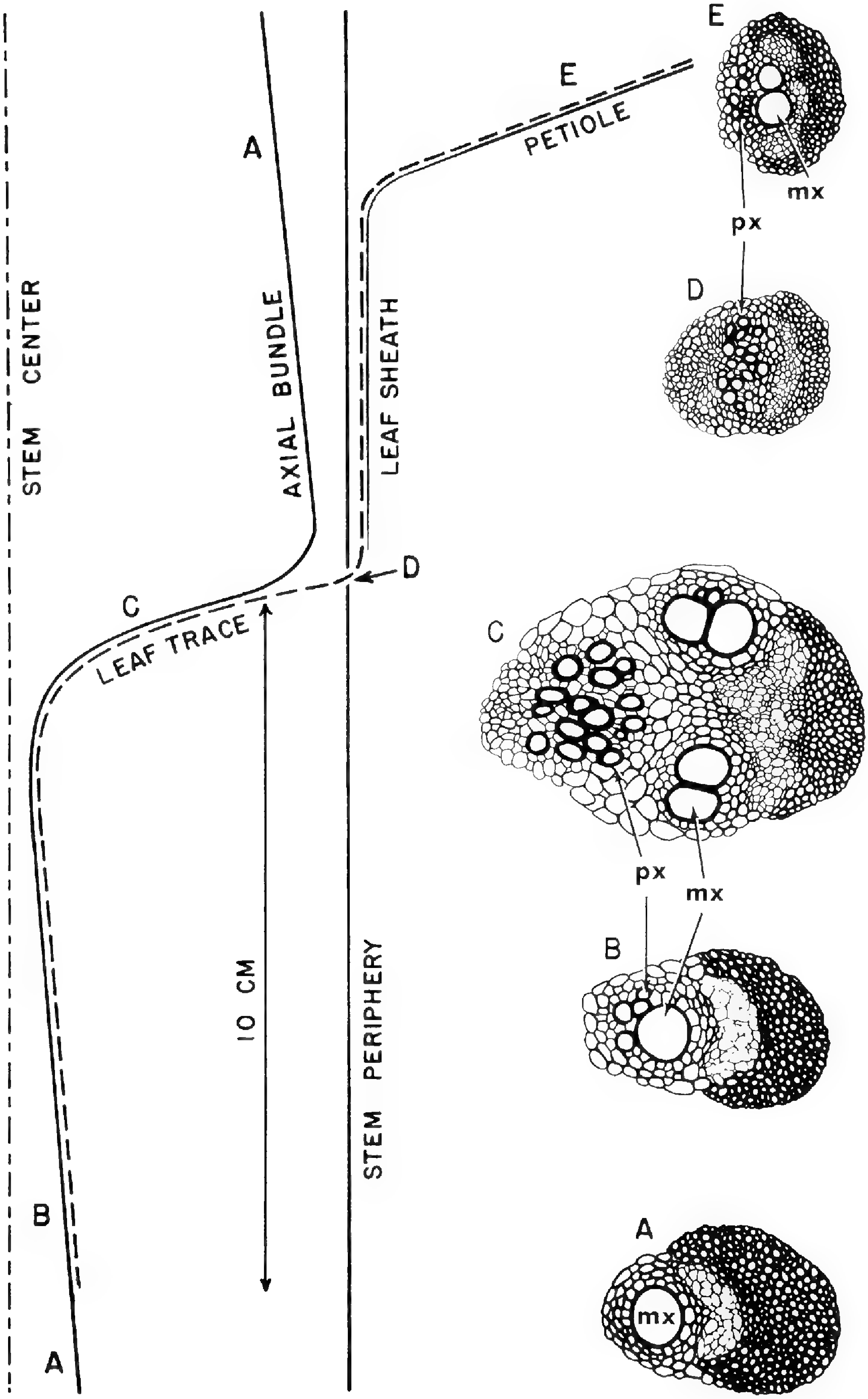
STEM CENTER
AXIAL BUNDLE
LEAF SHEATH
PETIOLE
LEAF TRACE
10 CM
STEM PERIPHERY
A
B
C
D
E
A
B
C
D
E
px
mx
px
mx
px
mx
mx

MATERIALS AND METHODS

Greenhouse-grown *Rhapis excelsa* (Thunb.) Henry plants from the Harvard Forest in Petersham, Massachusetts, and field-grown plants from the Fairchild Tropical Garden in Miami were used in this study.

The anatomy of tracheary elements in the stem-to-leaf vascular connection was studied in macerated material. Macerations were made from mature tissue of the peripheral stem area and the base of the leaf sheath and were examined for those elements of narrow diameter that connect stem and leaf sheath (see FIGURE 1, at D). The stem macerations necessarily contained both stem-to-leaf xylem and xylem from narrow peripheral axial bundles. The macerations from the leaf sheath, however, contained only xylem from the stem-to-leaf connection. From the macerated material, elements could be classified as vessel members or tracheids. Secondary-wall structure, length, and outside diameter of the elements were recorded, and many elements were photographed. Although inside diameter is relevant for hydraulic analysis, it is difficult to see in macerated material.

The distinction between metaxylem and protoxylem in the leaf insertion was made from both structural and developmental information. We define protoxylem as the primary xylem that has reached maturity before the surrounding tissue has ceased elongation, and metaxylem as that maturing after elongation is complete, even though it may begin to differentiate much earlier. Secondary-wall structure of tracheary elements provides only circumstantial evidence for distinguishing between protoxylem and metaxylem as thus defined. In the macerations tracheary elements with annular or helical secondary thickenings were regarded as protoxylem, and elements with pitted walls were assumed to be metaxylem.

To demonstrate the distribution of metaxylem and protoxylem in the leaf insertion more conclusively, we studied the relationship of xylem maturation to leaf elongation. Rate of elongation for the sheath, petiole, and subtending stem combined was determined from repeated measurements of the distance between the insertion of the lamina on the petiole and a reference point on the mature stem. These measurements were made on the four uppermost leaves with expanded laminae. Elongation of the petiole was similarly determined from reference points marked on it in waterproof ink. Extension growth of the sheath or stem alone was impossible to measure; one cannot dissociate the extension of the leaf sheath from the extension of its associated internode because of the overlapping leaf bases. Leaf axes (sheath and petiole) or petioles that had recently ceased elongation were sectioned by hand, and the sections were stained in phloroglucinol–concentrated HCl. In a given section of this

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FIGURE 1. Diagrammatic representation of departure of leaf-trace bundle in *Rhapis excelsa*. Solid lines in curves A-B-C-A and D-E indicate presence of metaxylem vessels; dashed lines, narrow protoxylem tracheids. Transverse sections of vascular bundles (A–E, right) correspond to positions A–E in curves on left; mx = metaxylem, px = protoxylem. Structure shown in diagram repeats itself axially, as indicated by 2 positions marked A.

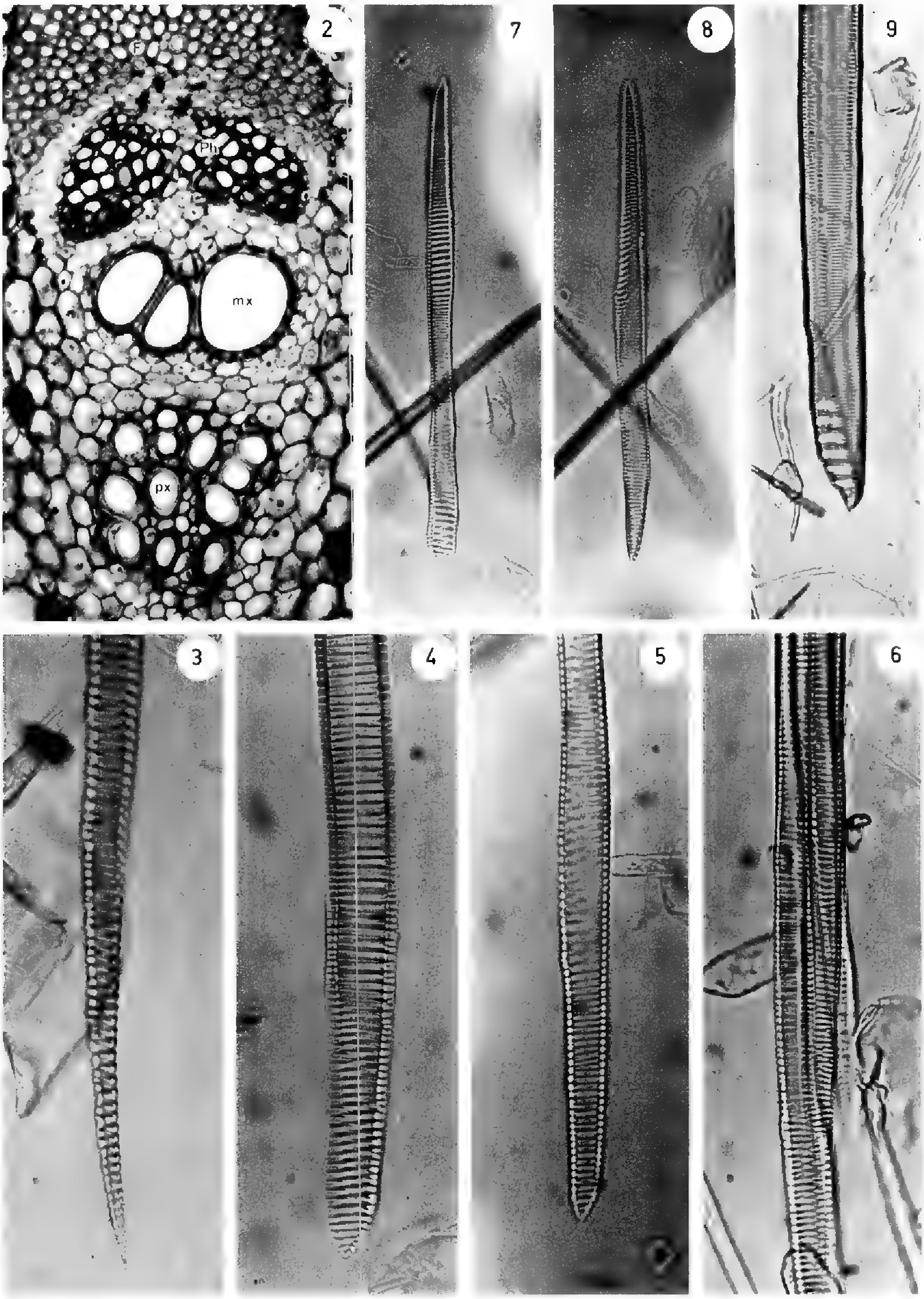
nonelongating tissue, metaxylem was indicated by immature tracheary elements (those with thin and nonstaining walls). Any fully mature elements (those with thick, stained walls) in the same section must represent protoxylem. Partially mature elements (those with intermediate wall characteristics) in the section were assumed to be transitional between protoxylem and metaxylem. These were always located between the mature and immature elements.

Vessel- and tracheid-length distributions were measured with the latex paint–infusion technique of Zimmermann & Jeje (1981). Dilute latex paint was injected into a cut stem for several days; paint-filled vessels were then counted with the aid of a stereo microscope on transversely cut surfaces at various distances from the point of injection. Vessel-length distribution in the vessel population of the stem was calculated from these counts. In our experimental material protoxylem elements were so narrow that they could not be resolved by the stereo microscope in transverse view. We therefore prepared relatively thick transverse sections so that paint-filled elements could be counted with the compound microscope. Each transverse section was cut into ca. 2-mm-wide strips; by counting piece after piece, it was possible to keep track of which parts of the section had already been counted.

Relative conductance per unit length of the xylem was determined at points along the vascular path from stem to lamina base in the following manner (see FIGURE 10, below). Petioles of leaves that had completed their extension were sectioned transversely from the base of the sheath to the lamina at 2-cm intervals. From these sections, inside diameters of all tracheary elements wider than ca. 12 μm were measured (smaller-diameter elements are hydraulically insignificant). The sums of all fourth powers of inside tracheary diameters were then calculated for each transverse section to yield a figure proportional to the conductance per unit length, according to the Hagen-Poiseuille equation of laminary flow. This assumes that all conduits are ideal capillaries, which is not strictly true (Zimmermann, 1983). Relative conductances along the vascular path were then plotted, based on the conductance arbitrarily taken as equal to one at the point of leaf attachment. Because the xylem connection between stem and leaf is extremely complex (Zimmermann *et al.*, 1982), the relative conductance value of the stem is based on the comparison of a single large metaxylem vessel of an axial bundle with a single leaf trace at the leaf insertion. This comparison is possible because we know that each leaf trace is ultimately continuous with a single axial bundle (see FIGURE 1). We did not determine the relative conductance of the leaf traces between the base of the sheath (D in FIGURE 1) and their junction with the metaxylem of axial bundles (approximately C to B in FIGURE 1) because of the difficulty in distinguishing the total complement of these traces from other bundles in the stem.

RESULTS

The structure of the leaf-trace complex in the stem has been studied previously (Zimmermann & Tomlinson, 1965; Zimmermann *et al.*, 1982) and is summarized for a single leaf-trace bundle in FIGURE 1. A vascular bundle at A contains only metaxylem vessels (mx) and is called an axial bundle. These



FIGURES 2–9. 2, transverse section of leaf trace in stem. Large metaxylem vessels (mx) continuous within stem; smaller tracheids (px) connect stem with petiole (F = fibers, Ph = phloem), × 260. 3, 4, tips of protoxylem tracheids with helical secondary-wall thickening, × 130. 5, tracheid with helical secondary wall at tip and reticulate secondary wall along main part of body, × 130. 6, cluster of tracheids (note matching position of their secondary walls), × 130. 7, 8, vessel element in macerate of leaf base shown from 2 different angles; scalariform perforation plate at lower end at very tip of element, upper one about ⅓ down from tip, × 230. 9, relatively wide vessel element of leaf sheath near insertion, × 230.

normally contain a single vessel, except where vessel ends overlap. If one follows such an axial bundle acropetally, one eventually detects a few protoxylem elements (px). This point is located at least 10 cm below the departure of the leaf trace. At B a few narrow px elements are present. Some of these px elements are in lateral contact with the wide mx vessel.

As one moves acropetally along the bundle from B to C, the number of px elements seen in transverse section increases. This is true to a lesser extent of the mx vessels as well. Lateral contact between px and mx is present to a point somewhere between B and C. At C the px is completely isolated laterally from the mx, even though both systems are within the same vascular bundle.

The isolation of px from mx below C marks the beginning of the leaf trace proper. FIGURE 2 shows a leaf trace in a stem transverse section corresponding to level C in FIGURE 1. If one follows such a leaf trace acropetally, one can see that the large metaxylem vessels (mx) continue up the stem within an axial bundle branch (A in FIGURE 1) and bridges (not shown in FIGURE 1, but see Zimmermann & Tomlinson, 1965), and that the narrow protoxylem (px) tracheary elements continue as a leaf-trace bundle that enters the leaf base (at D in FIGURE 1) (Zimmermann *et al.*, 1982). Thus, the leaf base is supplied by protoxylem only.

This paper primarily concerns the xylem of the leaf trace in the leaf-insertion region. This is the area of the leaf trace between its beginning as isolated px in the vascular bundles of the stem (C in FIGURE 1; FIGURE 2) and its course through the basal part of the leaf sheath. The term "leaf insertion" refers to the organographic junction of leaf and stem (D in FIGURE 1), not to the vascular junction. The vascular junction of leaf and stem is the region of contact between px and mx in the vascular bundles of the stem (between B and C in FIGURE 1). The xylem of the leaf trace in the leaf-insertion region contains narrow tracheary elements that suggest the presence of a hydraulic constriction for xylem sap entering the leaf.

ANATOMY OF THE TRACHEARY ELEMENTS

The macerated tissues from both the peripheral stem area and the lowermost part of the leaf sheath included parenchyma cells, fibers, and tracheary elements—the latter the objects of our attention. Even in stem macerations one can easily recognize protoxylem elements of outgoing leaf traces by their narrow diameter and annular or helical secondary wall structure, although there may be a few additional axial elements of narrow peripheral axial bundles. In macerations from the basal part of the leaf sheath, we are dealing exclusively with xylem that is continuous from stem to leaf.

The macerated material from both the stem periphery and the leaf sheath contained many tracheids about 1 mm long. The shortest one recorded was 425 μm; the longest (in the leaf base), 2.8 mm. Tracheids tended to be somewhat longer in the leaf sheath than in the stem, and their outside diameters ranged from ca. 23 to ca. 40 μm. Most tracheids had helical secondary walls throughout their length and were assumed to be protoxylem (FIGURES 3, 4, 6). There were others, however, with helical secondary walls at their tips and reticulate walls in their middle sections (FIGURE 5). These tracheids are apparently transitional between metaxylem and protoxylem. No tracheids with entirely reticulate walls were found. We did find reticulate-walled vessel elements of narrow diameter, which we classified as metaxylem. Some were of narrow, long, tracheidlike shape with scalariform perforation plates (FIGURES 7, 8); others were wider, but still with scalariform perforation plates (FIGURE 9). In the stem preparations we could not be sure whether these apparent metaxylem vessels were from stem-to-leaf xylem or from narrow peripheral axial bundles. Their presence in the leaf base, however, suggested that both protoxylem and metaxylem contribute to the bottleneck of the leaf insertion.

Extension-growth studies provided more direct evidence for the presence of metaxylem in the leaf-insertion region. As expected, elongation of the petiole ceased basipetally, and this was assumed to be the case for the sheath as well. Total elongation of the petiole, the leaf sheath, and the subtending stem ceased in the second-youngest expanded leaf. Anatomical examination of the leaf insertion of the second-youngest expanded leaf revealed narrow metaxylem elements (as indicated by their immaturity in the nonelongating tissue). Such elements are presumably destined to become those that we saw as narrow, reticulate-walled vessel members in the maceration of the mature leaf base. This metaxylem extends from the very base of the sheath into the petiole (solid line from D to E in FIGURE 1). Comparative structural examination indicated that metaxylem maturation is basipetal and is not complete until the leaf is the fourth expanded one in the crown. There was no indication of metaxylem in the area of the leaf trace between the axial bundle junction and the base of the sheath (ca. C to D in FIGURE 1).

Length distributions of the wide metaxylem vessels of the central cylinder of the stem have been reported before (Zimmermann *et al.*, 1982). In another set of latex paint–infusion experiments, we measured the length distribution of the tracheids and vessels in the peripheral stem area. We counted a total of 1843 perfused narrow conducting units (tracheids and vessels) in the stem. Counts at 1-mm intervals yielded the following length distribution: 55 percent, lengths shorter than 1 mm; 35 percent, 1–2 mm; and 10 percent, longer than 2 mm and up to several cm. From our maceration results it was obvious that the two shortest length classes (0–1 and 1–2 mm) concerned tracheids and the longer length classes concerned primarily vessels, although there are a few tracheids exceeding 2 mm in length. Length distributions of the conducting units in the sheath and petiole concerned only metaxylem vessels and were similar in both regions. Roughly 85 percent of the vessels were shorter than 1 cm; the remaining were mostly shorter than 5 cm, with a few as long as 9 cm.

DIMENSIONS OF THE STEM-PETIOLE CONNECTION

Cursory observation revealed that there are more narrow tracheary elements at the leaf insertion than in the petiole. In a typical case the total number of tracheary elements (per transverse section) at the leaf insertion was a little over 200, but in the first 2 cm of the leaf sheath above the insertion it decreased to about half that number and then remained roughly constant along the length

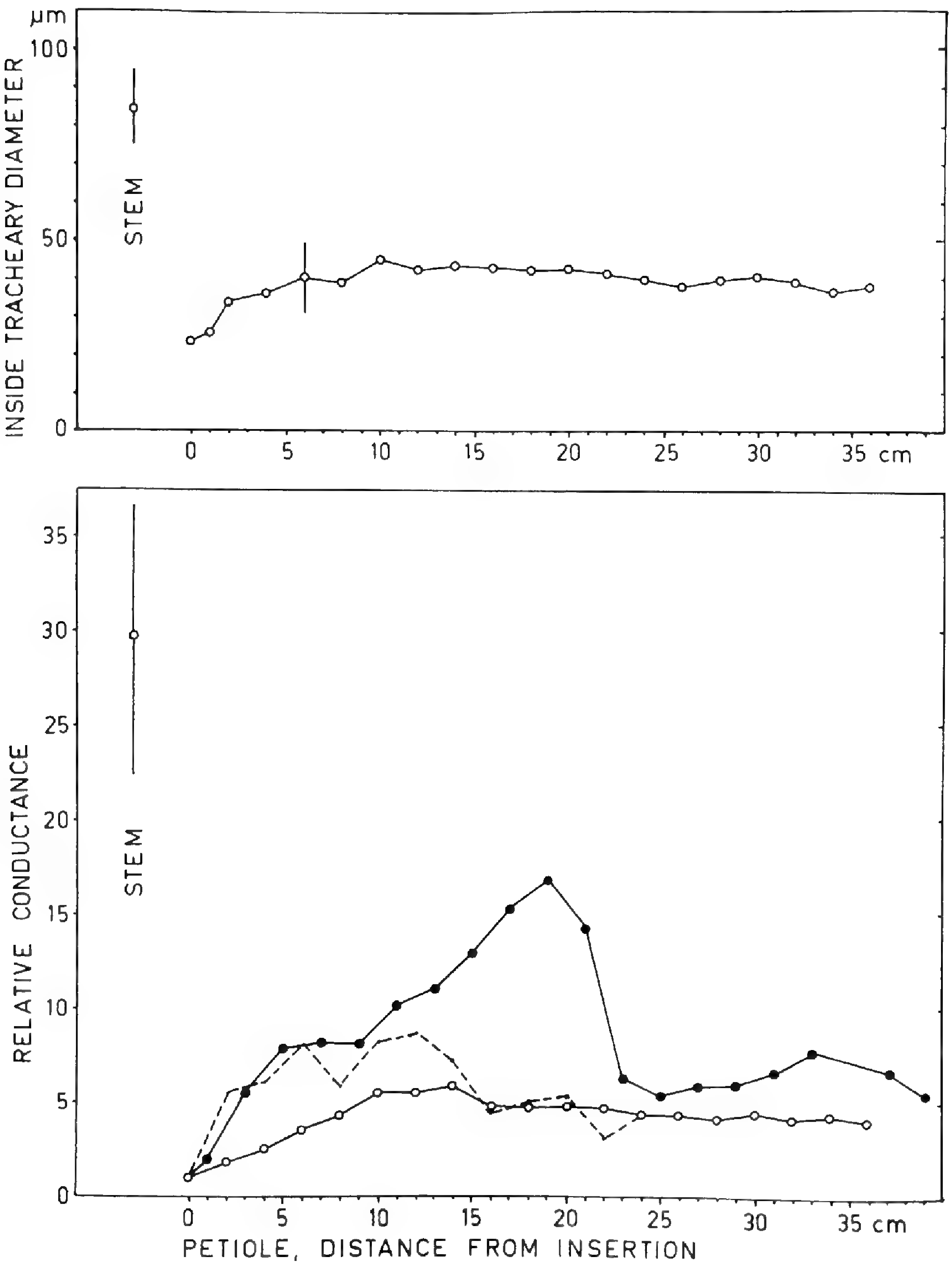


FIGURE 10. Above: average inside diameters of all tracheary elements wider than 12 µm, from insertion at stem (0 cm) along petiole (narrower ones hydraulically insignificant). Average diameter of large vessels in stem given at left for comparison. Vertical bars = standard deviations. Below: calculated relative conductances (per unit length) of xylem at points along vascular path from stem to lamina base, with conductance = 1 at leaf insertion (0 cm). Values for petioles (including leaf sheath) from 3 different plants. Average value for stem shown on left.

of the petiole. The diameters of the tracheary elements in each bundle increased from an average of 24 μm at the insertion to ca. 35 μm within the petiole (FIGURE 10). Absolute values of these dimensions varied from leaf to leaf, and among different shoots, but relationships within a plant were quite constant.

FIGURE 10 also shows the relative conductance along a typical mature stem-to-leaf connection for three leaves. Plainly, the observed bottleneck at the insertion is quantitatively significant. Conductance is highest in the stem and lowest at the insertion; it increases distally in the petiole to a value somewhat below that of the stem. The magnitude of the constriction would probably be even greater if the area of the leaf trace that is solely protoxylem (between C and D in FIGURE 1) could have been measured. The bottleneck is consistently present in all leaves examined, although its magnitude varied somewhat from leaf to leaf. The meaning of this variation is unknown, but it may be correlated with leaf position. Leaves low on the stem seem to have less of a bottleneck (Sperry, unpubl.).

Although based on precise measurements, FIGURE 10 shows a somewhat theoretical result. We know that the hydraulic constriction at the leaf insertion must be greater than FIGURE 10 indicates. There are four reasons for this. 1) The area of the leaf trace (roughly 4 cm) between C and D in FIGURE 1 could not be included in the calculations for technical reasons mentioned. Because this stretch is constituted wholly of protoxylem, it probably has a conductance as low as or lower than that determined for the base of the leaf sheath. 2) The region between B and C in FIGURE 1, where water must pass from the large metaxylem vessels to the narrow contiguous protoxylem tracheids, offers additional resistance to flow. The amount of resistance afforded by this crossover is unknown, but it may be considerable. 3) The xylem of the insertion consists primarily of tracheids, while in the stem and petiole most of the water moves through vessels. Tracheids are less efficient conductors than vessels, regardless of diameter. 4) Some of the protoxylem tracheids are certainly nonfunctional because they have been stretched and superseded by later-formed tracheids and vessels. These should not have been counted, but it was not possible to recognize nonfunctional tracheids in transverse sections. We must therefore assume that the actual hydraulic constriction at the leaf insertion is greater than is indicated by FIGURE 10.

DISCUSSION

Our observations provide evidence for a considerable hydraulic constriction in the xylem path between stem and petiole. It is caused in part by the absence of metaxylem from the area of the leaf trace between the junction of the axial bundle and the base of the sheath (the dashed line between C and D in FIGURE 1). Small metaxylem vessels, however, continue the constriction at the base of the leaf sheath (the solid line immediately above D in FIGURE 1). From the base of the leaf sheath to the petiole, conductance increases due to the presence of ever-wider metaxylem vessels (FIGURE 10). The fact that metaxylem contributes to the structure of the constriction suggests that this constriction is not merely a consequence of a developmental constraint (the inability of the plant to make wide protoxylem), but that it is an integral part of the vascular design and has adaptive value. We suggest that this hydraulic constriction at the leaf insertion plays a critical role in confining cavitation and subsequent conduction failure to areas beyond the stem, thereby insuring the functional integrity of the stem xylem.

If we assume that the likelihood of cavitation in a tracheary element increases with increasing sap tension and increasing tracheary diameter (given that the pore sizes in the tracheary walls are all the same (Zimmermann, 1983)), the quantitative anatomy presented in this paper indicates that vulnerability to cavitation is highest in the petiole, or possibly in the leaf blade. The reduced conductance at the insertion indicates a sharp pressure drop from stem to petiole when sap is flowing. Consequently, under transpirational conditions, xylem sap in the petiole will always be at considerably lower pressure than in the stem. Even in the absence of a constriction, xylem pressure in the petiole will be slightly lower than that in the stem, but the constriction introduces a sharp drop and thus greatly increases the pressure difference under conditions of flow. In addition to being at relatively low (negative) pressures, the sap in the petiole must flow in wide metaxylem vessels. Thus, relatively high tension is combined with wide vessels in the middle of the petiole. For this reason, we believe that in time of water stress, cavitations may be largely confined to the wide vessels of the petiole. Conduction in the xylem of the expendable leaf will be sacrificed to preserve the function of the xylem of the stem.

The leaf-trace structure illustrated for *Rhapis* in FIGURE 1 is similar to that in other palms (Zimmermann & Tomlinson, 1974). If the hydraulic architecture of other palms acts as we believe it does in *Rhapis*, it confines cavitations to the leaves. If no dependable mechanism is available to palms for the reversal of cavitation, the hydraulic constriction at the leaf base may be a necessary condition for the survival of palms. Less dramatically, it may also be responsible in part for observed patterns of leaf longevity in palms. Although some palms (e.g., arecoid palms with a crownshaft like *Roystonea*) abscise their leaves while they appear to be still healthy, when *Rhapis* and many other palms are grown under ideal (humid) conditions, the older leaves merely dry out. In these latter species, hydraulic architecture may be the mechanism responsible for the sequence of events. As a seedling palm grows taller, its stem must share the water supply with more and more leaves. Xylem pressures drop. Furthermore, if progressively more vessels in the petiole cavitate as the leaf ages, older leaves will have more vapor-blocked vessels than younger ones. This will increase the resistance to flow in old leaves, which may in turn increase the likelihood of cavitation. Hydraulic constriction may therefore favor young—and discriminate against old—leaves. Xylem failure in older leaves would happen more rapidly under unfavorable (dry) conditions. This would explain the fact that while *Rhapis* plants grown outdoors in the sun carry only a tuft of leaves at the top of the stem, those grown in a greenhouse and watered regularly retain leaves along a much greater length of the stem.

The hypothesis put forth in this paper is consistent with the available anatomical data and certain commonplace observations of palm growth. We hope that it is a promising step toward a more complete analysis of how palm xylem functions in sap conduction and palm growth.

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CABOT FOUNDATION
HARVARD UNIVERSITY
PETERSHAM, MASSACHUSETTS 01366

NEW SPECIES OF TIMONIUS (RUBIACEAE) FROM PAPUASIA

STEVEN P. DARWIN

TIMONIUS DC., the largest genus of tribe Guettardeae, is confined to the paleotropics from the Seychelles eastward through Malesia and tropical Australia to Micronesia and the South Pacific, with the center of diversity in New Guinea. During recent studies of the genus, several new species have been discerned from herbarium material available for examination. Although a revisionary study of the entire genus is planned, the new species are proposed here since the monographic treatment will probably require a concerted effort of several years. I am grateful to the directors and curators of the cited herbaria for making specimens available for loan. This research was partially supported by grant DEB-8102781 from the National Science Foundation. The delimitation and sequence of Papuasian geographic regions employed in this study follow those of Coode (Brunonia **1:** 131–302. 1978).

Timonius zuckianus S. Darwin, sp. nov.

Ex affinitate speciebus foliis paxillatis praesertim T. longifolii Valeton sed floribus longioribus, fructibus magnis, foliorum laminis apice abrupte acute acuminatis et cymis glabris differt.

Shrub or tree to 20 m tall. Branchlets 2–5 mm broad toward apex, compressed but becoming terete, gray, glabrous except puberulent above stipule scars; stipules imbricate, lanceolate, acuminate, to 130 by 15 mm, glabrous without, glabrous within except for slender colleters toward base. Leaves with petiole stout, semi- to sub-terete and somewhat winged by leaf blade, 12–55 mm long, ca. 2 mm broad at middle, glabrous; blade elliptic, 7–13 by 3–7.5 cm, abruptly and sharply acuminate at apex, obtuse at base or decurrent onto petiole, coriaceous, glabrous on both surfaces, the costa plane or canaliculate above, prominent beneath, the lateral nerves indistinct, the veinlets paxillate, prominulous-striate above, prominulous or subplane beneath, the domatia resembling small pits, glabrous or minutely puberulent, dispersed over lower surface. Staminate cymes 5- to 7-flowered, at anthesis to 3 by 3 cm; peduncles stout, compressed, 6–10 by up to 3 mm, glabrous; bracts none; calyx tube cupular, truncate to undulate, (1–)2–3 mm high, glabrous, the basal portion (aborted ovary) to 1.5 mm high; corolla narrowly infundibular, the tube 8–12 by ca. 1.5 mm, glabrous inside and out, the limb 12–18 mm broad, the lobes 4, ovate, 6–8 by 3–4 mm, acute, somewhat irregular at margin; stamens 4, the anthers 5–6 by ca. 0.5 mm, glabrous, included. Pistillate cymes 2- or 3- (or 4-)flowered,

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at anthesis to 3.5 by 2 cm, the peduncles stout, compressed, 8–18 by up to 3 mm, glabrous; bracts none; calyx tube cupular, truncate to undulate, 0.5–1 mm high, glabrous; corolla subhypocrateriform, the tube 5–7 by ca. 1.5 mm, glabrous inside and out, the limb to 12 mm broad, the lobes 6 to 8, ovate, to 5 by ca. 1.5 mm, acuminate, somewhat irregular at margin; staminodia 6, ca. 3 by 0.5 mm, glabrous, included; ovary and disc glabrous, the style glabrous, unequally 6-branched, slightly exserted. Fruits short-cylindric to depressed-globose, 6-sulcate, 4–5 by 6–7 mm, glabrous, crowned by persistent calyx; pyrenes 35 to 45, vertically oriented and arranged in 6 radiating double files.

Type. Normandy Island, Mt. Pabinama, 820 m alt., 2 May 1956, *Brass 25653* ♀ (holotype, A!; isotypes, CANB!, LAE!).

Distribution. Islands of extreme southeastern Milne Bay Province of Papua New Guinea.

Ecology and field notes. Common in lower montane forests and stunted mossy forests of ridge-crests from 700 to 1700 m alt. Ranging in habit from a shrub or small tree of about 2 m to a canopy tree 20 m tall. Bark rough, dark brown; wood white to pale straw-colored. Probably flowering and fruiting throughout the year. The pistillate and staminate flowers are reported as white, the fruits as black and fleshy when mature.

Specimens seen. **Papua.** Papuan Islands: Goodenough Is., E slopes, *Brass 24525* ♀ (A, CANB, LAE); Fergusson Is., Mt. Kilkerran, E slopes (Woiatabu), *LAE 71045* ♂ (A, BISH, LAE); Tagula Is., Mt. Riu, W slopes, *Brass 27839* ♀ (A, LAE), Mt. Emuwa, *LAE 74520* ♀ (BRI, CANB, LAE); Rossel Is., Kwa mountain above Abilete, *NGF 27077* ♀ (A, BRI, CANB, LAE), Mt. Rossel, summit, *Brass 28458* ♀ (A, BO, LAE), Mt. Rossel, S slopes, *Brass 28389* ♂ (A, BO, LAE).

Timonius zuckianus is allied to the other species of the genus in which lateral or secondary nerves are only weakly developed, with the paxillate veinlets forming a striate pattern on the upper leaf surfaces in herbarium specimens. In addition, the calyces are truncate and stipules are imbricate in bud. The present species is unusual in its exceptionally large flowers and more prominently acuminate leaf apices. It resembles *T. longifolius* Valeton, from the Sepik area of New Guinea, in its cymose pistillate inflorescences (in all other species of this alliance the pistillate flowers are solitary), but its larger fruits, glabrous inflorescences, and elliptic rather than oblanceolate leaves suggest *T. singularis* (F. Mueller) L. S. Sm., from Australia.

I take pleasure in naming this distinctive species for Dr. and Mrs. Robert K. Zuck, formerly of Department of Botany, Drew University, who inspired many college students to pursue botanical careers.

Timonius pubistipulus S. Darwin, sp. nov.

Ex affinitate speciebus foliis paxillatis praesertim T. belensis Merr. & Perry sed stipulis intus minimum in centro vel basin versus dense pallidis sericeis differt.

Epiphytic shrub or terrestrial tree to 35 m tall. Branchlets 3–4 mm broad toward apex, compressed but becoming terete, either glabrous except puberulent above stipule scars or conspicuously pubescent; stipules imbricate, lanceolate, to 80 by 15 mm, long-acuminate, glabrous without, toward center or base densely pale-sericeous within. Leaves with petiole stout, semi- to subterete, 4–20 mm long, 1.5–2 mm broad at middle, glabrous; blade elliptic to obovate, 4–12 by 1.5–5.5 cm, acute to short-acuminate at apex, acute to subattenuate at base, rigidly coriaceous, glabrous above and beneath, the costa canaliculate above, prominent beneath, the lateral nerves hardly distinguishable, the veinlets paxillate, subplane to prominulous on both surfaces, the domatia resembling small pits, glabrous to minutely puberulent. Staminate cymes 3- to 5-flowered, in bud ca. 1.5 by 1 cm; peduncles stout, subcompressed, 3–5 by 1.5–2 mm, glabrous; bracts none; calyx tube cupular, truncate to obscurely obtuse-denticulate, 0.5–2 mm high, glabrous; corolla narrowly infundibular, the tube to 8 by ca. 1.5 mm, glabrous inside and out, the limb to 5 mm broad, the lobes 4, lanceolate, ca. 3.5 by 1 mm, sharply acuminate; stamens 4, the anthers ca. 6 mm long, glabrous. Pistillate flowers solitary; peduncle compressed, 1–5 by 1–2 mm, in fruit to 12 mm long; glabrous; bracts none; calyx tube cupular to cylindrical, truncate to undulate, 0.5–1 mm high, glabrous; corolla broadly infundibular, the tube (3–)5–7 by 2–2.5 mm, sometimes somewhat broader in throat, glabrous inside and out, the limb to 8 mm broad, the lobes 6 or 8, lanceolate, 2.4–3.5 by 1–1.5 mm, conspicuously acuminate; staminodia 6, ca. 2 mm long, glabrous, included; ovary subglobose, 3–3.5 by 3–4 mm, glabrous like the disc, the style 6- to 8-branched, subexserted. Fruits subglobose to broadly obovoid and somewhat laterally compressed (when dried appearing distally sulcate and proximally tuberculate), 6–9 by 7–10 mm, glabrous, crowned by persistent calyx; pyrenes 30 to 45 in transverse section, ca. 10 in vertical section, probably up to 60 per fruit, subvertically oriented.

I am readily able to distinguish two varieties within this species.

Timonius pubistipulus var. **pubistipulus**

T. avenis sensu Merr. & Perry, Jour. Arnold Arb. **26:** 235. 1945, *pro parte, non* Valeton.
T. carstensensis sensu Merr. & Perry, Jour. Arnold Arb. **26:** 238. 1945, *pro parte, non* Wernham.

TYPE. Papua New Guinea, Western Highlands Province, Minj River valley above the Nona River camp, in *Nothofagus* forest at 9000 ft alt., 30 July 1957, *Pullen 268* ♀ (holotype, A!; isotypes, BISH!, BM!, BO!, BRI!, CANB!, G!, LAE!).

DISTRIBUTION. Interior of North East New Guinea and Papua.

ECOLOGY AND FIELD NOTES. In montane *Araucaria*, *Nothofagus*, and moss-forests or swamps, 350–3400 m alt.; most collections from above 1500 m alt. Epiphytic shrubs, "climbers," or trees to 30 m tall with trunk diameters to 0.5 m, frequently in forest edges, burnt-over areas, and other open habitats. The bark surface varies from gray and smooth to brownish and pustular or scaly; the wood is white to reddish straw-colored; the stipules frequently reddish and conspicuous. Staminate and pistillate flowers vary in color from white to greenish, yellowish, or rarely pinkish, with the corolla lobes often paler than the tube; mature fruits are dark red to black. Flowering and fruiting throughout the year.

Vernacular names. "Komai" (Kiliga), "Kormai" (Enga), "Kumai" (Hagen, Kiliga, Togoba), "Kume" (Mendi), "Kumeh" (Onim), or "Ome" (Mendi); "Haikapula" (Ialibu); "Abalan" (Enga); "Moghon" (Nerenavip); "Sikil" (Togoba); "Takuneh" (Naho); "Torobin-kama" (Sinasina-Nimai); "Tombarumb," "Tombumpf," or "Tomburump" (Minj); "Yambasi" (Fiyugi).

Specimens seen. **North East New Guinea.** West Sepik: S of Nerenavip, Hindenburg Range, *NGF 32144* ♀ (A, BRI, CANB, LAE), *NGF 32181* ♂ (A, BRI, CANB, LAE). Madang: S slopes Finisterre Range to S of Mt. Abilala, *Pullen 6132* ♀ (CANB, L, LAE). Morobe: Mannasat, Cromwell Mts., *Hoogland 9600* ♀ (A, BRI, CANB, LAE); Sarawaket, *Clemens 5758* ♀ (A); summit of Mt. Shongul, *NGF 37434* ♂ (LAE); New Yamap, *NGF 27552* ♀ (A, BRI, CANB, LAE, SING); Aseki Road, ca. 57 km from Bulolo, *LAE 75226* ♀ (LAE, UPNG); Angabena ridge near Haumuga, Aseki area, *Schodde & Craven 4743* ♀ (A, BRI, CANB, L, LAE); Edie Creek road above Wau, *NGF 13489* ♀ (BRI, CANB, LAE); Bulldog Road ca. 20 km S of Wau, *Fallen 550* (LAE); above Bakaia, ca. 15 mi SW of Garaina, *Hartley 12716* ♀ (A, BRI, CANB, L, LAE). Western Highlands: Sirunki, Marapamanda, E of Laigam and N of Yamara, *ANU 762* ♀ (A, CANB, LAE); N slopes of Sugarloaf complex along Wapu R., *Hoogland & Schodde 7089* ♀ (A, BM, BRI, CANB, LAE, Z); ca. 5 mi N of Londoli, Ambum Valley on Wabag–Maramuni Road, *Saunders 1013* ♂ (CANB, LAE); River Kum, Mt. Kum, *LAE 50320* ♀ (A, CANB, LAE); Tomba, *NGF 35512* ♂ & ♀ (LAE); top of Mt. Oga, *Saunders 677* (A, BM, LAE); slopes of Mt. Kinkain, Kubor Range, *Saunders 741* (CANB); upper Nona R., *Saunders 747* (A, BM, BRI, CANB, LAE), *Saunders 748* (CANB); Minj-Nona Divide, N side of Kubor Range, *Pullen 5167* ♀ (A, BRI, CANB, LAE); Kubor Ranges above Kuli, *Robbins 524* ♀ (LAE). Eastern Highlands: 2 mi SW of Koge Mission, Sinasina, *Hide 309* ♀ (LAE), *Hide 486* (LAE). **Papua.** Southern Highlands: Mimimbipl, 20 mi from Mendi, Tambul Road, *LAE 55321* ♀ (A, BISH, LAE); W slope of Mt. Giluwe above Klareg, *Schodde 2015* ♀ (A, BRI, CANB, LAE); SW slope of Mt. Giluwe, *Schodde 1673* ♂ (A, CANB, LAE); base of Mt. Giluwe, *LAE 74437* ♀ (BRI, CANB, LAE); slopes of Mt. Giluwe, *NGF 32502* ♀ (A, BRI, CANB, LAE, SING); Omin, *ANU 20326* (LAE); near Capuchin Mission sawmill, N side of Pangia Road 4 mi E of Ialibu, *UPNG 4224* ♀ (UPNG). Central: E of Mt. Tafa, *Brass 4077* ♀ (BRI); Mt. Tafa, *Brass 5046* ♀ (BO, BRI); road from Woitape to Kosipi, Iowasi Swamp, *NGF 20308* ♀ (A, BO, BRI, CANB, LAE, SING); E slope Lake Myola no. 2, *NGF 34629* ♀ (A, BISH, LAE); Koitaki, *Carr 12522* ♀ (A, BM, CANB, SING); Boridi, *Carr 13095* ♀ (A, CANB, SING), *Carr 13343* ♀ (A, BM, CANB, SING), *Carr 14607* ♂ (A, BM, CANB); Lala Valley, *Carr 15856* (BM, L, SING); The Gap, *Carr 15042* ♂ (A, BM, SING); above The Gap, *Carr 13819* ♀ (A, BM, CANB, K); Sogeri region, *Forbes 770* ♀ (A, BM, L). Northern: Kokoda, *Carr 16453* ♀ (B, CANB), *Carr 16478* ♂ (CANB, G). Milne Bay: junction Ugat and Mayu rivers near Mayu 1, *NGF 28897* ♀ (A, BISH, CANB, LAE, SING); Mayu 2, Mt. Suckling, *LAE 54117* ♀ (A, CANB, LAE); Goropu Mts., Pumpunipon to S ridge of Goe Dendeniwa, *Veldkamp & Stevens 5694* ♂ (BISH, L, LAE); track, S spur to Pumpunipon, Mt. Suckling complex, *LAE 54178* ♀ (CANB, LAE); N slopes of Mt. Dayman, Maneau Range, *Brass 22304* ♀ (A, CANB, LAE), *Brass 22702* ♀ (A, CANB, LAE), *Brass 22874* ♀ (A, CANB, LAE); Mt. Dayman, *Paijmans 1090* ♀ (CANB); Mt. Wadimana, NE outlier of Mt. Simpson, *Pullen 7842* ♂ (A, LAE); summit area, Mt. Wadimana, *Schodde 5472* ♂ (CANB, L, LAE); Aparamu Ridge, E of Mt. Simpson Range, *Schodde 5519* (CANB).

Timonius pubistipulus var. **pubescens** S. Darwin, var. nov.

Omnio idem ac varietas typica sed ramuli pubescentia conspicua et plus minusve persistenti differt.

Type. Papua New Guinea, Morobe Province, Mt. Kaindi near Edie Creek, heavy liana in a *Nothofagus* forest, 7900 ft alt., 9 May 1963, *Hartley 11840* ♀ (holotype, A!; isotypes, C!, CANB!, G!, L!, LAE!).

Distribution. Interior of eastern West New Guinea, North East New Guinea, and Papua.

Ecology and field notes. Montane forests, 1500–2600 m alt.; mainly in swamps, myrtaceous scrub, edges of trails, ridge-tops, old landslides, and other open or successional habitats. Varying in habit from epiphytic shrubs to lianas or slender trees to 25 m tall with trunk diameters to 25 cm. The bark surface is pale gray to dark brown and smooth, the wood white to pale brown. The flowers are yellowish or brownish white, rarely dull pinkish, and the fruits are maroon to black when mature. Flowering and fruiting throughout the year.

Vernacular name. "Komai" (Enga).

Specimens seen. **West New Guinea.** Snow Mountains: Bijenkorfbivak, Helling Hellwigberg, *Pulle 773* (A, L). **North East New Guinea.** West Sepik: Folongonom, second bush camp below Tamanagabip on track to Busilmin, *LAE 59483* ♀ (A, BISH, LAE). Morobe: NE slope of Mt. Rawlinson, *Hoogland & Craven 9341* ♀ (A, BM, BRI, CANB, K, LAE); Ogeramnang, *Clemens 4649* ♀ (A, B); Aseki-Spreader Divide, *LAE 54772* ♀ (A, BISH, CANB, LAE); E slope Spreader Divide, ca. 7 mi NW of Aseki, *Schodde & Craven 4904* ♀ (A, BRI, CANB, LAE); near Wengomanga, via Oiwa, *Craven & Schodde 1291* ♀ (CANB, LAE); along water race of N. G. Mine, *NGF 21063* ♀ (A, BISH, BRI, CANB, LAE, SING); Edie Creek, *NGF 19948* (CANB, LAE), *NGF 19959* ♀ (A, BISH, BO, BRI, CANB, LAE, SING), *Hartley 11725* ♂ (A, BRI, CANB, LAE); Mt. Kaindi, SE slope, *Allison NG-195* ♀ (LAE); track descending SE from S summit of Mt. Kaindi, *UPNG 3114* (UPNG); ca. 14 km WSW of Wau, Mt. Kaindi, *Allison NG-171* ♀ (LAE); Mt. Kaindi summit, *NGF 13908* ♀ (A, BO, BRI, CANB, K, LAE); Kaindi, *Brass 29559* ♀ (A, BO, CANB, LAE), *Brass 29561* ♂ (A, CANB, LAE); ca. 15 km SSW of Wau, Bulldog Road, *WEI 1374* ♀ (LAE); Bulldog Road, 12 km SSE of Wau, *Pratt NG-105* ♀ (LAE); Bulldog Road ca. 13 km SSE of Wau, *Allison NG-161* ♀ (LAE); Lake Trist, *NGF 29135* ♀ (A, BRI, CANB, LAE, SING); 5 km E of Lake Trist, *Paijmans 1568* ♀ (CANB, LAE). Western Highlands: top of ridge 3 mi S of Kompiam, *ANU 2805* ♀ (A, CANB, K, LAE). Eastern Highlands: confluent Warapuri and Kori rivers, Wahgi-Jimmy Divide, N of Nondugl, *NGF 18173* ♀ (BRI, CANB, LAE); summit Mt. Elandora, *Jermy 5025* ♀ (LAE). **Papua.** Southern Highlands: Onim, *Rau 160* ♀ (LAE). Western: Mt. Bosavi, N side, *Jacobs 8859* ♀ (BISH, L, LAE). Northern: E side of Lake Myola no. 1, *LAE 61972* ♂ (BISH, BO, CANB, LAE, MO, SING).

Timonius pubistipulus, clearly allied to other paxillate-veined species of the genus, is most closely related to *T. belensis* Merr. & Perry, with which it is sympatric in the western part of its range. However, the present species is readily distinguishable from all other "paxillate" species by its stipules, which are conspicuously and densely pale-sericeous on the inner (adaxial) surface. Although the extent of the stipular pubescence varies, I have had no difficulty assigning specimens here. Most pistillate material can be recognized as belonging to *T. pubistipulus* on the basis of the subvertically arranged pyrenes; these are intermediate between the very oblique pyrenes of *T. belensis* and the strictly vertical ones of such other species as *T. avenis* Valeton.

Timonius pubistipulus var. *pubescens* differs from the typical variety in its branchlets that are usually conspicuously brown-pubescent, at least when young.

rather than glabrous. This is a feature shared with *T. trichanthus* Merr. & Perry, although that species has pubescence extending to the outer surfaces of stipules and lower surfaces of leaf blades, as well as other distinguishing characters. On the basis of available collections, it appears that var. *pubescens* extends farther west but not so far east as var. *pubistipulus*, but the varieties are sympatric through most of their range and occupy similar habitats.

Timonius subavenis (Valeton) S. Darwin, comb. nov.

Timonius scaber Valeton var. *subavenis* Valeton, Bot. Jahrb. **61**: 51. 1927.

Epiphytic shrub, or at maturity small tree. Branchlets 2–3 mm broad toward apex, compressed but becoming terete, pubescent with scattered, spreading, brown hairs; stipules imbricate, lanceolate, to 45 by 10 mm, acuminate, abaxially hirsute toward base and center with somewhat shaggy brownish hairs but usually glabrous toward margin, adaxially glabrous except for scattered colleters. Leaves with petiole slender, 5–15 mm long, 1–2 mm broad at middle, hirsute; blade long-elliptic to oblanceolate, 4–14 by 3–7.5 cm, at apex long-acuminate to sharply acute, at base cuneate and decurrent, thinly coriaceous to chartaceous, above short-pubescent when young, soon glabrous except base of costa, beneath sparsely to densely appressed or spreading brown-pubescent, the costa plane to canaliculate above, prominent beneath, the lateral nerves obscure above, submerged beneath, the domatia absent. Staminate cymes 3- to 11-flowered, at anthesis 1.5–3 by 1.5–2.5 cm; peduncles 2–8 by ca. 1.5 mm, densely tomentose to subglabrous; bracts absent; calyx cupular, truncate, the limb about 0.5 mm high, glabrous, the basal portion (abortive ovary) about 1 mm high, pubescent but at very base glabrous and constricted; corolla narrowly infundibular, the tube to 10 mm long (late bud), densely hirsute outside with distally pointing hairs, probably glabrous inside, the lobes 4. Pistillate flowers solitary; peduncle to 5 by ca. 2 mm, puberulent with scattered hairs to glabrous; bracts not seen; calyx tube cupular, truncate, about 0.5 mm high, glabrous; corolla narrowly infundibular, the tube 6–7 mm long, to 1.5 mm broad at middle, hirsute outside, probably glabrous inside, the limb 5–6 mm broad, the lobes 6, to 2 mm by ca. 1 mm, acute; ovary subglobose, 3–3.5 by 3–3.5 mm, pubescent with scattered long hairs to glabrous. Fruits subglobose, somewhat laterally compressed, 4–5 by 3.5–6 mm, 6- to 8-ribbed, pubescent like ovary, crowned by persistent calyx and disc; pyrenes to 45 per fruit, vertically oriented, arranged in 6 to 8 radiating double files corresponding to ribs.

TYPE. The identity of Valeton's species *Timonius scaber* is as yet uncertain since I have not located any material of *Ledermann 13086* (pistillate), the only collection cited (Bot. Jahrb. **61**: 50. 1927). Variety *subavenis* would seem even more mysterious since no collection at all was cited, but one staminate specimen, *Ledermann 8793* (SING!), is annotated "Timonius scaber var. subavenis n. sp." on a Berlin Museum label, possibly in Valeton's hand. This I designate the lectotype of *T. scaber* var. *subavenis*, here elevated to specific rank. The lectotype agrees well with Valeton's unusually brief description. It bears only the locality "Sepik-Gebiet," but was probably collected in the vicinity of Malu and April River (Fl. Males. **1**: 317. 1950).

ECOLOGY AND FIELD NOTES. Ranging in habit from an epiphyte to a liana, shrub, or small tree. The few available collections were made in primary forests and swamp forests at 50–1750 m alt. Staminate and pistillate flowers are white to reddish. Flowering and fruiting throughout the year.

SPECIMENS SEEN. **West New Guinea.** SNOW MOUNTAINS: Bijenkorfbivak, Zuidhelling Hellwigberg, *Pulle 650* ♂ (A, BO, L, SING); Pesechem-vallei, *Pulle 1155* ♂ & ♀ (BO, L). DJAJAPURA: Rouffaer R., *Docters van Leeuwen 10141* ♀ (A, BO, K, L), *Docters van Leeuwen 10172* ♂ (BO, K, L); Bodem R., 60 km SE of Sarmi, *BW 8101* ♀ (BR, CANB, LAE); Bernhard bivouac, *Meyer Drees 499* ♂ (A, BO, K, L, SING), *Meyer Drees 607* ♂ (BO, L).

Timonius subavenis is similar to *T. trichanthus* Merr. & Perry but occupies a more westerly range. As in *T. trichanthus,* stipules and corollas (staminate and pistillate) are pubescent outside, the fruits are sulcate with the pyrenes arranged vertically, and the staminate inflorescences have fewer than 15 flowers. The differentiating characters lie mainly in the calyces: in *T. trichanthus* the basal portion (ovary or abortive ovary) is glabrous or nearly so (vs. pubescent in *T. subavenis*) while the calyx tube is pubescent and 1 mm or more high (vs. glabrous and about 0.5 mm high in *T. subavenis*). In addition, the pistillate peduncles are somewhat longer in *T. trichanthus.*

Timonius paiawensis S. Darwin, sp. nov.

Ex affinitate T. laevigati Valeton sed foliorum nervis lateralibus utrinque 5–7 supra impressis infra prominentibus differt.

Shrub or slender tree to 8 m tall. Branchlets 3–5 mm broad toward apex, compressed but becoming terete, yellow-puberulent; stipules valvate, deltoid, to 15 by 5 mm, acute, minutely and densely puberulent without, densely yellow-hirsute within. Leaves with petiole rigid, semiterete, 5–20 by 1–3 mm, glabrous to subpuberulent; blade narrowly elliptic to suborbicular, 7–18 by 2.5–12 cm, gradually or abruptly sharp-acuminate at apex, narrowly to broadly cuneate at base, subcoriaceous, glabrous and glossy above (dark when dried), glabrous or with small hairs scattered over lamina and frequently denser on costa and nerves beneath, the costa plane to canaliculate above, elevated beneath, the lateral nerves spreading, 5 to 7 on each side of costa, impressed above, prominent beneath, the veinlets subimpressed above, reticulate, the domatia inconspicuous in axils of lateral nerves. Staminate cymes to 20-flowered, at anthesis ca. 2 by 2–3 cm; peduncles stout, 3–15 by ca. 2 mm, yellow- to brown-puberulent; bracts broadly clasping, to 3 by 5 mm, rounded at apex, pubescent, caducous, probably a larger, caducous, opposite pair enclosing young inflorescence (not seen); calyx narrowly ellipsoid to ovoid, in bud 4–7 mm high, the limb irregularly 5-toothed, often rupturing laterally; corolla (seen in bud) yellow- to red-puberulent, the lobes 5. Pistillate flowers solitary; peduncle 4–15 (–22) by ca. 2 mm, yellow-puberulent; bracts connate, calyptrate, to 8 mm long, puberulent, caducous, affixed beneath ovary; calyx tube ca. 2 (3–5 in fruit) mm high, distally contracted and confluent with top of ovary, 6-toothed or somewhat erose; corolla narrowly infundibular, the tube ca. 8 by 2 mm, pale sericeous without, probably glabrous within, the limb ca. 10 mm broad, the lobes 6, narrowly lanceolate, ca. 4 by 1 mm, acute; style pubescent. Fruits subglobose to obturbinate, 9–14 by 9–14 mm, densely yellow-puberulent, crowned by persistent calyx; pyrenes ca. 25 in transverse section, ca. 18 mm long, obliquely oriented in reddish pulp, surrounded by firm mesocarp 1–2 mm thick.

TYPE. Papua New Guinea, Morobe Province, 10 mi up Paiawa River, low shrub or small tree, 20 October 1965, *NGF 25030* ♀ (holotype, A!; isotypes, BISH!, BRI!, CANB!, LAE!, SING).

ECOLOGY AND FIELD NOTES. Shrubs or slender trees apparently confined to riverine habitats, from sea level to 600 m alt. The bark surface is reported as gray to brown, smooth or somewhat vertically fissured; the wood is white to brown. The flowers are noted as white to greenish or brownish, and the fruits are reddish when mature. Flowering and fruiting between May and October.

SPECIMENS SEEN. **North East New Guinea.** MOROBE: Baden Bay, Buso, *NGF 39097* ♂ & ♀ (A, BRI, CANB, LAE); Buso, *NGF 47767* ♀ (A, BISH, BO, BRI, CANB, LAE); near Buso, growing on Buso R., *LAE 52328* ♂ & ♀ (A, BISH, LAE), *Conn et al. 301* ♀ (A); Buso Forestry Camp, *Conn 313* ♀ (A, CANB); Paiawa Valley, *NGF 47318* ♀ (BISH, BO, BRI, CANB, GH, LAE), *NGF 47326* ♂ (LAE); Saru R., 7 mi SE of Garaina, *NGF 47993* ♀ (A, BISH, BO, BRI, CANB, LAE).

Timonius paiawensis is similar to *T. laevigatus* Valeton in its coriaceous leaves, yellow-pubescent branchlets, deltoid, valvate stipules, and denticulate calyces that in pistillate specimens are more or less confluent with the top of the ovary in the young bud. The leaves of *Timonius laevigatus*, however, have more numerous lateral nerves that are neither impressed above nor strongly elevated beneath. Furthermore, the two species have very different geographic ranges: *T. laevigatus* extends from the Sepik region of Papua New Guinea westward, while *T. paiawensis* seems confined to Morobe Province.

DEPARTMENT OF BIOLOGY
TULANE UNIVERSITY
NEW ORLEANS, LOUISIANA 70118

TWO UNUSUAL CHIONANTHUS SPECIES FROM BORNEO AND THE POSITION OF MYXOPYRUM IN THE OLEACEAE

RUTH KIEW

CHIONANTHUS Linnaeus (including *Linociera* Sw.—Stearn, 1976), with about 70 species described, is the largest genus of the Oleaceae in Malesia but the least well known. As study of the genus progresses, it is possible to appreciate the range of variation within the genus; for example, study of the Malayan species shows that there are intermediate species with characters of both sections CERANTHUS Bentham & Hooker and EULINOCIERA Bentham & Hooker (Kiew, 1979), and investigation of the Bornean species reveals a much wider range in inflorescence and fruit form than was previously described (Kiew, 1980).

THE PROBLEM OF LINOCIERA MACROBOTRYS

In the revision of the Sarawak species (Kiew, 1980), specimens of *Linociera macrobotrys* Merr. were not available for study. On the grounds of two unusual characters for the genus—its habit (it is a shrub 2 m tall) and its terminal inflorescence—the species was excluded from the genus with a note that its description closely matched that of *Myxopyrum enerve* Van Steenis. In the Kew and Leiden herbaria, specimens identified as *L. macrobotrys* are in fact the small-leaved form of *M. enerve.*

The type of *Linociera macrobotrys* was subsequently traced to the herbarium of the Arnold Arboretum. Examination showed that the inflorescence is not terminal but axillary, and that the flowers are all staminate (a character not mentioned in Merrill's description (1918)).

The tendency toward unisexual flowers is seen in several Malesian genera of the tribe Oleeae Bentham & Hooker. *Olea* L. has polygamous species. *Osmanthus* Lour. generally has unisexual flowers (Green, 1958), although the Malesian species, *O. scortechinii* King, is hermaphrodite. The vast majority of *Chionanthus* species have hermaphrodite flowers, but polygamous species do exist (for example, the well-known Chinese fringe tree, *Chionanthus retusus* Lindley & Paxton, and *C. enerve* (see below)). There are also unisexual species such as *Linociera oxycarpa* Lingelsh. and *L. rupicola* Lingelsh., both from New Guinea, and *C. macrobotrys,* as yet known only from a staminate specimen from Sarawak.

Lingelsheim (1927), in his study of the Oleaceae in New Guinea, mentioned that the polygamous and unisexual *Chionanthus* species, in which the filament is fused to the corolla, could be distinguished from those of *Olea,* in which the

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filament is free. In all Malesian species of *Chionanthus* investigated so far (both those with hermaphrodite and those with staminate flowers), the filament is always short and is fused near the base of the corolla. The connective varies in width (FIGURE 1, d–i) and is apiculate in some species (FIGURE 1, g). With the exception of *O. paniculata* R. Br. (FIGURE 1, c), in which the filament is not only free from the corolla but also versatile, the Malesian *Olea* species have similar stamens with short filaments fused to the corolla (FIGURE 1, a, b). Staminal characters can therefore not be used as a generic distinction between *Chionanthus* and *Olea*.

Chionanthus macrobotrys has staminate flowers and oblong corolla lobes with a rounded apex, which are also found in the *Olea* species in Borneo, *O. decussata* (Heine) Kiew and *Olea javanica* (Blume) Knoblauch. *Chionanthus macrobotrys* is distinguished from these *Olea* species by the absence of the rounded bud characteristic of *Olea* and by the corolla that is divided more than halfway. These characters confirm this taxon as a species of *Chionanthus*.

Chionanthus macrobotrys (Merr.) Kiew, comb. nov.

Linociera macrobotrys Merr. Philipp. J. Sci. **13:** 117. 1918. TYPE: Sarawak, 1st Division, Mount Poe [Gunung Pueh], *Foxworthy 369* (A).

Shrub 2 m tall. Twigs terete, brown becoming grayish with age, minutely hirsute. Leaves with petiole 5 mm long; blade lanceolate, 5–5.5 by 2–2.5 cm, acute at apex, entire and recurved at margin, cuneate at base, coriaceous, minutely punctate below, glabrous; midrib impressed above, with lateral veins ca. 4 pairs, obscure above and below. Inflorescence a lax panicle with fourth-order branching, axillary, minutely hirsute, 14.5 cm long, lowest second-order branches 9 cm long; bracts oval, 2–3 mm long. Staminate flowers yellowish, 2 mm long; pedicel 2–3 mm long; calyx 0.5 mm long, deeply divided to base, lobes acute, glabrous; corolla 2 mm long, lobes 1 mm long, induplicate-oblong with rounded apex, joined in pairs for 1 mm at base; stamens 2, connate to base of corolla, the anthers almost sessile, to 1 mm long, connective ca. 0.5 mm wide. Ovary absent. Pistillate or hermaphrodite flowers and fruits unknown.

This description differs in two important respects from that of Merrill: the inflorescence is axillary (not terminal as Merrill reported), and the flowers are staminate. The species is known from a single locality, Gunung Pueh, and Merrill cited two specimens, *Foxworthy 369* (type) and *290*; I have not been able to locate the latter. On the herbarium label Foxworthy noted that the plant grows in forests on the upper slopes of the mountain between 1500 and 1700 m. He gave "barungian batu" as the Dyak name.

Among the Bornean *Chionanthus* species, *C. macrobotrys* most resembles *C. ramiflorus* Roxb. in its rounded corolla lobes (FIGURE 1, e, h) and in its lax, much-branched panicle. However, the flowers of *C. ramiflorus* are hermaphrodite and the leaves are larger. Merrill (1918) considered the leaves of *C. macrobotrys* to be unusual in their small size and coriaceousness, but those of the montane form of *C. laxiflorus* Blume and the small-leaved form of *C. enerve* are very similar. Of the Bornean species other than *C. macrobotrys*, only *C. longipetalus* (Merr.) Kiew is a shrub.

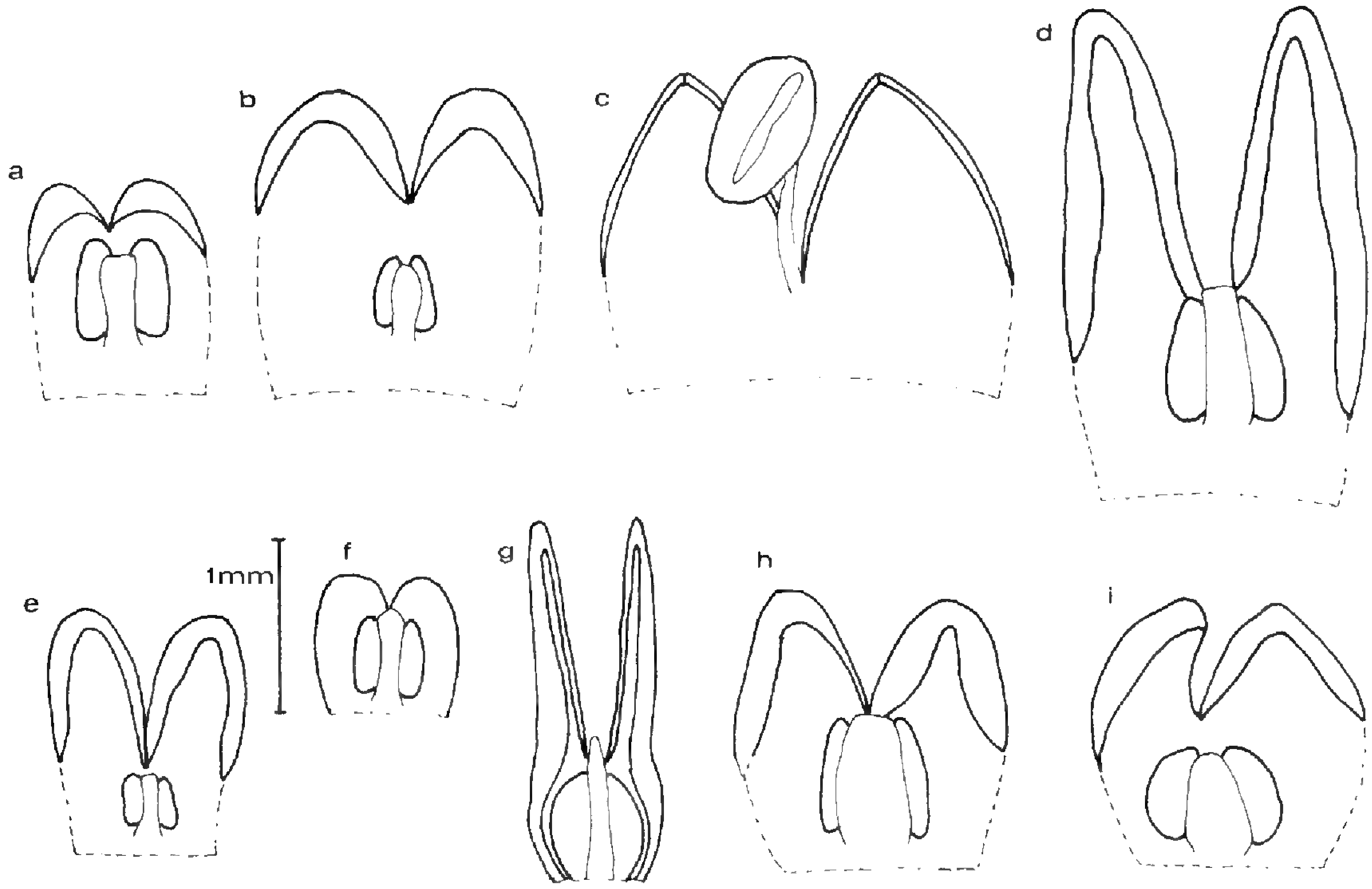

FIGURE 1. Stamen attachment in staminate and hermaphrodite flowers of *Olea* and *Chionanthus* (including *Linociera*): a, *Olea decussata* (staminate, *Chew 939*); b, *O. brachiata* (hermaphrodite, *Ahmad s.n.*); c, *O. paniculata* (hermaphrodite, *Schodde & Craven 5061*); d, *Chionanthus porcatus* (hermaphrodite, *Anderson 20044*); e, *C. ramiflorus* (hermaphrodite, *Van Royen & Sleumer 6939*); f, *Linociera oxycarpa* (staminate, *NGF 42633*); g, *L. rupicola* (staminate, *TGH 13667*); h, *C. macrobotrys* (staminate, *Foxworthy 369*); i, *C. enerve* (staminate, *Collenette 905*).

THE PROBLEM OF MYXOPYRUM ENERVE

The matching descriptions of *Linociera macrobotrys* (which *is* a species of *Chionanthus*) and *Myxopyrum enerve* Van Steenis and the identification of specimens of *M. enerve* as *L. macrobotrys* have led me to reexamine the position of *M. enerve*. *Myxopyrum enerve* is atypical of *Myxopyrum* Blume in that its leaves are not triplinerved and its stem is terete.

This species also differs in its leaf anatomy from *Myxopyrum coriaceum* Blume and *M. nervosum* Blume. In these *Myxopyrum* species foliar sclereids are confined to below the midrib and only brachysclereids are present; in *M. enerve* there are dendrosclereids throughout the lamina (FIGURE 2, C) as well as brachysclereids in the midrib and the petiole. In both *M. coriaceum* and *M. nervosum* the xylem forms several discrete blocks in the petiole; in *M. enerve* it is crescent shaped (FIGURE 3). In addition, there is a difference in position of the ovules—pendulous in *M. enerve* and ascending in *M. coriaceum* and *M. nervosum* (although Van Steenis (1967) reported that the specimen of *M. nervosum* he had examined had pendulous ovules).

In all these characters, *Myxopyrum enerve* resembles *Chionanthus* and not *Myxopyrum*. Species of *Chionanthus* have pinnate venation, terete stems, dendrosclereids in the lamina, crescent-shaped xylem in the petiole (Kiew & Ibra-

FIGURE 2. Cross sections of laminae: A, *Myxopyrum coriaceum* (*S 25442, Anderson*), × 370; B, *M. nervosum* (*Henderson 32382*), × 370; C, *Chionanthus enerve* (*S 22740, Asah Luang*), × 185.

him, 1982), corolla lobes longer than the tube, and pendulous ovules. Herbarium specimens of *M. enerve* also have black petioles, a character found in *Chionanthus* but not in *Myxopyrum.* The small flowers fall within the range of flower size for *Chionanthus* (2–9 mm long; Kiew, 1980). Two characters unusual for *Chionanthus* are the scandent habit and the terminal inflorescence. However, another Bornean species, *C. longipetalus* (Merr.) Kiew, is a shrubby species that has once (*S 21498, Ashton*) been recorded as climbing, and *C. retusus* has a terminal inflorescence. For all these reasons, *M. enerve* is undoubtedly a species of *Chionanthus.*

Chionanthus enerve (Van Steenis) Kiew, comb. nov.

Myxopyrum enerve Van Steenis, Blumea **15:** 152. *fig. 3.* 1967. TYPE: Sarawak, 4th Division, Gunung Dulit, *S 22740, Asah Luang* (holotype, L).

Woody scandent climber 2–5 m long. Twigs terete, lenticellate, drying gray. Leaves with petiole 0.5–1.5 cm long, grooved above, drying black; blade ovate-lanceolate, 4.5–12.5 by 1.5–6.5 cm, acute to acuminate at apex, truncate to rounded at base, entire and recurved at margin, thickly coriaceous, glabrous, punctate below toward base of leaf; midrib depressed above, prominent below, with lateral veins 5 to 8 pairs, slightly impressed above and below. Inflorescence paniculate, terminal in flower but becoming displaced to lateral position in fruit, 4–12 cm long, once branched, lowest branches less than half length of inflorescence; bracts foliaceous, 4–7 by 1–3 mm. Flowers polygamous, greenish yellow, 1.5–2 mm long; pedicel 1–2 mm long; calyx 4-lobed, deeply divided to base, margin finely ciliate; corolla 1–2 mm long, lobes 4, induplicate, reaching to base, rounded at apex; stamens 2, the anthers almost sessile, 1.5 mm long, connective broad; ovary 1 mm long, ovoid, 2-loculate, each locule with 2 pendulous ovules, stigma 2-lobed; staminate flowers without vestige of ovary but otherwise similar. Fruits ovoid, 4–7 by 3–6 mm, minutely apiculate, green ripening purple, endocarp brittle; seed 1, endosperm copious.

HABITAT. Mossy forest on exposed summits or ridges, 780–2500 m; once recorded from mossy limestone cliff (Gunung Api).

VERNACULAR NAME. *Batu lawi* (Kelabit).

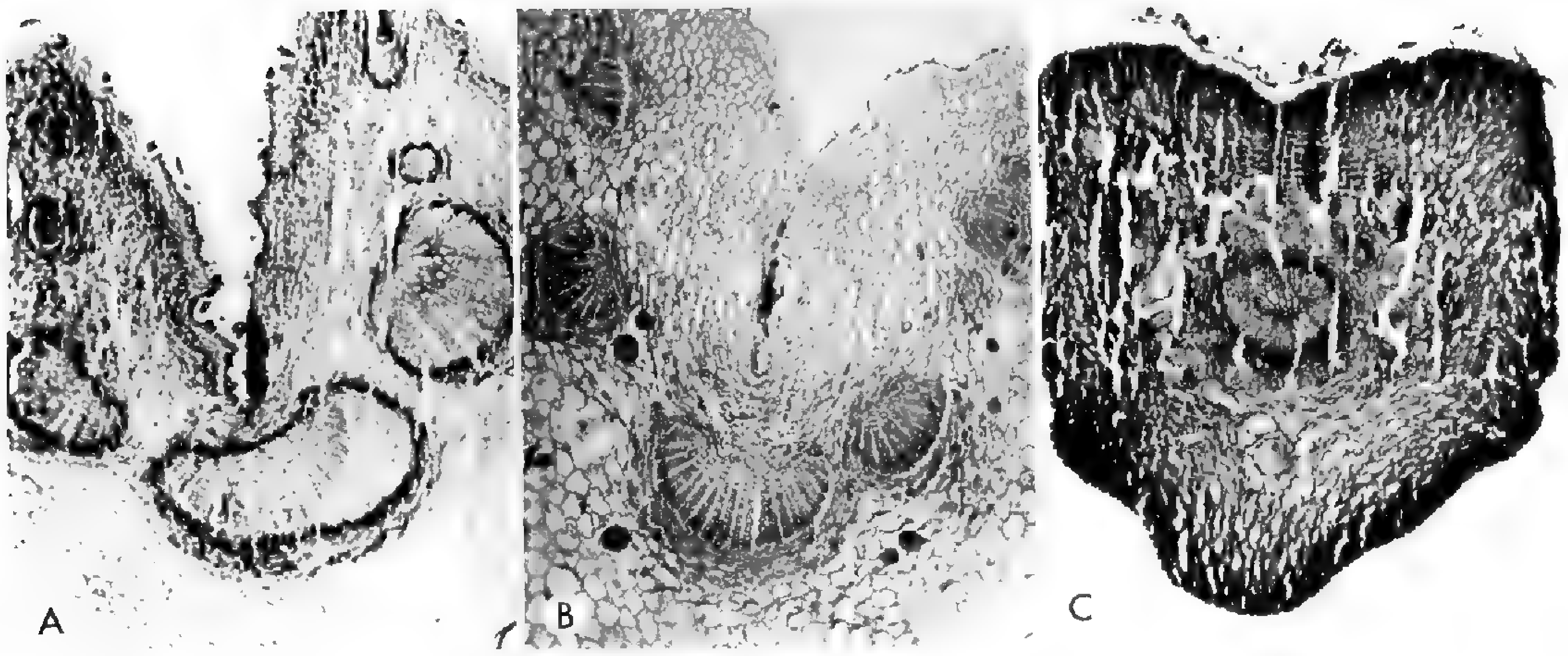

FIGURE 3. Cross sections of petioles: A, *Chionanthus enerve* (*S 22740, Asah Luang*), × 12; B, *Myxopyrum nervosum* (*Henderson 32382*), × 20; C, *M. coriaceum* (*S 25442, Anderson*), × 25.

SPECIMENS EXAMINED. **Borneo.** SABAH: Kinabalu, *Clemens 28777* (BO), *30910* (BO, K), *31442* (BO), *32834* (BO), *40183* (BO), *40704a* (K, L), *50128* (K), *51469* (K); *Chew & Corner 4499* (K); *Collenette 905* (K). SARAWAK. 1st Division: Gunung Santubong, *Martin S 37597* (SAR). 2nd Division: Lubok Antu, *S 33831, Chai* (KEP, SAR), *S 33950, Chai* (SAR), *S 33953, Chai* (SAR). 4th Division: Gunung Dulit, *S 22740, Asah Luang* (L); Gunung Api, *S 30433, Chai* (SAR); Kelabit Highlands, *Nooteboom & Chai 2263* (SAR). KALIMANTAN: Gunung Semedoem, *Hallier 688* (BO), *709* (BO).

Van Steenis (1967) based his description on a single specimen, but this species has been collected from exposed hilltops and ridges from 780 to 2500 m throughout Sarawak and Sabah. There is considerable range in leaf size (from that of the type specimen, 7.5–12 by 3–6 cm, to small-leaved plants such as *Clemens 40704a*, 4.5–7 by 1.5–2.75 cm) and inflorescence length (4 cm in *Clemens 40704a* vs. 7.5–9 cm in the type). Among the species from Sarawak, the combination of coriaceous, lanceolate leaves and paniculate inflorescence is found only in *Chionanthus laxiflorus. Chionanthus enerve* can be distinguished from this species by its scandent (vs. arboreal) habit, its terminal inflorescence with short lower secondary branches (vs. branches more than one-third the length of the inflorescence), and its elliptic (vs. obpyriform) fruit.

Although the type specimen has hermaphrodite flowers, other specimens (*S 30433, Chai,* and *Collenette 905*) have staminate flowers; the species is therefore polygamous.

POSITION OF MYXOPYRUM IN THE OLEACEAE

Bentham and Hooker (1876) recognized four tribes in the Oleaceae and placed *Myxopyrum* in tribe Oleineae together with *Olea* and *Ligustrum* L., which have induplo-valvate corolla lobes and albuminous seeds. Knoblauch (1895) recognized two subfamilies: Jasminoideae (containing the single tribe Jasmineae), with bilobed fruits and amphitropous or anatropous seeds; and Oleoideae (containing three tribes), with unlobed fruits and—except in *Mayepea* Aublet and *Myxopyrum*—pendulous seeds. *Myxopyrum* was isolated

TABLE 1. **Common characters of Myxopyrum and tribe Oleeae, compared with those of tribe Jasmineae.**

CHARACTER	MYXOPYRUM AND OLEEAE	JASMINEAE
Leaf	Simple	Unifoliate, trifoliate, or pinnate
Corolla		
Lobes	4	4 to 12
Tube	Medium to short or absent	Long to medium
Style	Medium to short or absent	Long to medium
Aestivation	Valvate (except in *Osmanthus*)	Imbricate
Fruit	Not bilobed	Bilobed
Flavones	Present	Absent

from the other genera in tribe Oleineae by its ascending anatropous seeds. Solereder (1891) wrote that ovule position in *Mayepea* (now *Chionanthus*) is not uniform and detailed three positions: pendulous (most species), attached laterally, and attached almost at the base. Van Steenis's report (1967) of pendulous ovules in *Myxopyrum nervosum* (I find them to be ascending) is another indication that ovule position should not be used as a key character in delimiting the subfamilies.

Johnson (1957) expanded the scope of subfamily Jasminoideae to include five tribes: Jasmineae Bentham & Hooker (the only tribe with bilobed fruits), Forsythieae H. Taylor ex L. Johnson, Fontanesieae H. Taylor ex L. Johnson, Schrebereae L. Johnson, and the monogeneric Myxopyreae L. Johnson (provisionally placed in the subfamily). His subfamily Oleoideae included only two tribes, Fraxineae (*Fraxinus* L.) and Oleeae (which in Malesia included *Chionanthus, Ligustrum, Olea,* and *Osmanthus*). The latter is a natural group characterized by two pendulous ovules in each locule of the ovary and by a basic chromosome number of 23.

Apart from its scandent habit and the position of its ovules, *Myxopyrum* has little in common with the Jasminoideae and in particular with *Jasminum* L., the other Malesian climbing genus. If a wider range of characters is examined (see TABLE 1), it is obvious that *Myxopyrum* has more in common with Johnson's tribe Oleeae than with the Jasmineae. If keyed out under his subfamily Oleoideae, *Myxopyrum* splits: species with a fleshy, urceolate corolla key out under *Noronhia* Stadm. ex Thou. (a similarity already noted by Blume, 1850), and those with the tube shorter than the lobes key out under *Olea* (*Tetrapilus* Lour.) and *Chionanthus* (*Linociera*). In addition, *Myxopyrum nervosum* has flavone (apigenin) glycosides that are present in genera of subfamily Oleoideae but absent in those of subfamily Jasminoideae (Harborne & Green, 1980).

Based on a combination of leaf, flower, and fruit characters, rather than on the single character of ovule position, *Myxopyrum* should be transferred to subfamily Oleoideae (Kiew, 1981). However, although *Myxopyrum* shows similarities to genera of tribe Oleeae, it is distinct in several respects. In addition to its climbing habit, quadrangular stem, triplinerved leaves, and ascending ovules, it differs from all other oleaceous genera in two other characters. The separate blocks of xylem (FIGURE 3) have not been recorded from other genera of the Oleaceae, which have either a medullated cylinder (reported from *Chionanthus, Fraxinus,* and *Osmanthus*) or crescent-shaped xylem (reported from *Chionanthus, Fontanesia* Labill., *Jasminum, Ligustrum, Notelaea* Vent., *Olea, Osmanthus, Phillyrea* L., and *Syringa* L.) (Metcalfe & Chalk, 1950; Kiew & Ibrahim, 1982). The flavones present in *M. nervosum* are three unidentified glycosides of apigenin not found in the other genera of Oleoideae so far investigated (Harborne, pers. comm.). The chromosome number of *Myxopyrum* is still unknown. Because of these distinct characters, *Myxopyrum* should be retained in the separate tribe Myxopyreae, which is included in subfamily Oleoideae.

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DEPARTMENT OF BIOLOGY
AGRICULTURAL UNIVERSITY OF MALAYSIA
SERDANG, SELANGOR, MALAYSIA

A NEW NAME IN SPERMACOCE FOR TWO SPECIES OF BORRERIA FROM NEW GUINEA

OSIA GIDEON

THE BORRERIA-SPERMACOCE PROBLEM has recently been the subject of much discussion by some of the keenest students of the Rubiaceae. For the last century *Spermacoce* L. and *Borreria* G. F. W. Meyer have been maintained as separate genera. The only difference between the two is whether one or both valves of the capsule dehisce; their general facies are so similar that a specimen without mature fruits cannot usually be referred to the proper genus with any certainty. I am not sure that this character is either good or constant enough to justify generic separation. Although it sounds defensible on paper, it is difficult to see; worse still, it is absent without ripe fruits. Verdcourt (Kew Bull. **30**: 301. 1975) reunited *Borreria* with *Spermacoce* and gave an excellent explanation of the problem in support of this viewpoint. Interested readers should refer to his paper. Since *Spermacoce* sensu lato (including *Borreria* as a section) is readily identifiable, I prefer this view and will treat New Guinea species accordingly. Fosberg (pers. comm.) has for many years (even before Verdcourt's reduction of *Borreria*) been using *Spermacoce* in its broad sense.

Merrill and Perry described two species of *Borreria* from New Guinea, *B. linearis* Merr. & Perry and *B. lanceolata* Merr. & Perry. These species, with bilocular capsules and both valves opening from the top to expose the seeds, undoubtedly belong to *Borreria* (= sect. BORRERIA (G. F. W. Meyer) Verdcourt). The main characters used to distinguish these two taxa were the erect habit of *B. lanceolata,* its lanceolate leaves, and its slightly larger flowers with corolla lobes definitely pubescent above. Study of numerous subsequent collections has shown that these distinctions are unreliable, and that a single variable taxon is represented. The habit of *Brass 11737* (the type of *B. lanceolata*) is not recorded on the field label; the specimen, with many long, rather slender stems branching near ground level, does not suggest an erect plant. The usual habit is decumbent to low spreading. The leaves vary little in shape: in *Brass 4067* (the type of *B. linearis*) many leaves have dried with the margins strongly curved, but some have remained flat and are distinctly lanceolate. Most leaves have short, stiff hairs along the midrib beneath, as well as on the margin (particularly near the apex). *Brass 11737* is the only collection that has no pubescence on the leaves. Flower size is rather variable and cannot be regarded as a reliable character. I have found no flowers in which the upper surfaces of the corolla lobes are glabrous. The seeds, although variable in size, are very uniform in appearance. In the absence of reliable distinctive characters, it seems wise to unite the two species under one name in *Spermacoce.* Although I have

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seen only the isotypes (from BRI), Mr. E. Henty, who has seen the holotypes, has kindly passed his notes on to me.

The specific epithets *linearis* and *lanceolata* cannot be used in *Spermacoce* due to the existence of several earlier names (*S. linearis* HBK. Nov. Gen. Sp. 343. 1818; *S. lanceolata* Link, Enum. Hort. Berol. **1:** 132. 1821; *S. lanceolata* Frank ex Presl, Bot. Bemerk. 86. 1844) that would make them later homonyms. It is therefore a pleasure to name the taxon after Dr. Leonard Brass, who collected the types of the original taxa. *Brass 4067* is here retained as the holotype since it is more representative of the species.

Spermacoce brassii Gideon, nom. nov.

Borreria linearis Merr. & Perry, Jour. Arnold Arb. **26:** 34. 1945. TYPE: [Papua New Guinea, Central District,] E of Mt. Tafa, 2350 m, *Brass 4067* (holotype, A; isotype, BRI).

Borreria lanceolata Merr. & Perry, Jour. Arnold Arb. **26:** 35. 1945. TYPE: [Indonesia, Irian Barat,] Balim River, *Brass 11737* (holotype, A; isotype, BRI).

DISTRIBUTION. New Guinea: along the central cordillera from Wissel Lakes (Irian Barat) to Mt. Donana (Milne Bay District), and the Saruwaged Range; 1300–3000 m alt.

DIVISION OF BOTANY
OFFICE OF FORESTS, DEPARTMENT OF PRIMARY INDUSTRY
P. O. BOX 314
LAE, PAPUA NEW GUINEA

INDEX

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Dates of Issue

No. 1 (pp. 1–169) issued 11 January 1983.
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Contents of Volume 64 *1983*

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CONTENTS OF VOLUME 64, NUMBER 4

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